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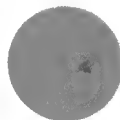
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Adaptations of birds to man-made environments
Ecology of raptors
Dynamics of birds ranges
Density regulation in bird populations
Ontogeny and phylogeny of cognitive processes
Physiology of the avian egg
Adaptive significance of colonies and flocks physiology of reproduction,
moult and migration
Avian respiration
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poster presentations, some full poster presentations, reports of round-
table discussions, the list of Congress Members

## ADAPTATIONS OF BIRDS TO MAN-MADE ENVIRONMENTS

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RAVKIN Yu.S.

ANTHROPOGENIC TRANSFORMATIONS OF AVIAN COMMUNITIES IN THE USSR FOREST ZONE

RUSTAMOV A.K.

BIRDS AND MAN-INDUCED ENVIRONMENTAL CHANGES IN THE ARID ZONE OF THE USSR

MORGAN R.

CHANGES IN THE BREEDING AVIFAUNA OF AGRICULTURAL LAND IN LOW-LAND BRITAIN

BLONDEL J.

MEDITERRANEAN BIRD FAUNAS IN THE LIGHT OF ANTHROPIC PRESSURE SINCE THE NEOLITHIC

TOMIALOJC L.

URBANIZATION AS A TEST OF ADAPTIVE POTETINALS IN BIRDS

DYRCZ A.

BREEDING ECOLOGY OF THE TWO POPULATIONS OF **TURDUS GRAYI** AT LOCALITIES OF DIFFERENT HUMAN INFLUENCE IN PANAMA LOWLAND

# ANTHROPOGENIC TRANSFORMATIONS OF AVIAN COMMUNITIES
# IN THE USSR FOREST ZONE

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The results of bird censuses in 328 habitats of East-European and Siberian forest zons, including some habitats of forested terraces of forest-steppe and secondary forest-steppe were analysed. All the censuses were carried out on the basis of method ( Ravkin, 1967 ) and cover more than 16.000 km from May 15th (or June 1st) to August 31st (1960-1981). In northern locations (sub-zones) the replacement of coniferous forests by mixed stand (which follows selective cutting) or by secondary overgrown extensive clearings and burns brings only insignificant change in values of diversity, bird community biomass, and transformed energy indices. In southern locations such as southern parts of boreal region, secondary forest-steppe and forested terraces of forest-steppe, however, the values of these indices clearly increase when calculated for early stages of succession on clsarings and burns, for mixed forests formed on older clearings and sometimes even partly ploughed areas. In such cases considerable changes in the species composition of predominating birds are also found. The decrease of these indices were observed on the stages of small-leaved forests for pasture digression and extensive fields. The construction of buildings leads to particularly pronounced increase in the summative community indices, except that of diversity, which esssntially decreases. For all that those changes are less in northern locations (subzones) that in southern ones.

Thus, anthropogenic transformation of forest bird communities is essential only in those cases when it is not within the framework of natural succession (forest maturation, pyrogenic succession or following the outbreak of pests), namely urbanization, pasture digression, extensive monocultural agroceonosis and, naturally, construction of hydro-electric power stations.

The factor analysis study had shown that in the bird communities of each locations (subzones) of West Siberia has three principal trends of changes. Former coincides with natural differences in woodiness from the forsèts of interstream areas, through the tessellated habitats to the bottomlands of large rivers.

The second trend coincides with differenses in productivity and damping. It's first row goes from the waterless vallsy's forests, through the damp and paludose forests to the wooded back fens and further to ths rised bogs. The second row coincides with environmental changss from the mosaic natural habitats of waterless valleys through fields with copses to the woodless transitional and rised bogs. The third row of this trend goes from the meadows, through the flood-land's back fens to the nonfloodland's back fens and further to the same opened transitional and rised bogs.

The third trend is connected with building. It goes from the flood-plains of large rivers, through the settlements in their ranges to the nonfloodland's villages and further to the outskirts of towns and urban parks, and further to the central part with multistory buildings.

The main changes in avian communities in the forest-steppe's pine forests are connected with discreasing of woodness also in three directions. The first as in the forest zone follows from the forests to the mosaic habitats and further to the bottomland meadows. The second is connected with impoverishment because of ploughing and pasture degression. The rows connected with damping are represented only by initial stage of conversion from bottom land meadows of large rivers to the opened back fens. The third trend, as in the forest zone is directed from the bottom land habitats in connection with buildings firstly of country (rural) type, further to the outskirts of towns and to the centre with multistory buildings. When the forests are occupied by gardens with temporary building or the forests are disposed in the middle of housing estates in the towns of diffuse type the latter begins from this habitats.

The quantative estimation of anthropogenic influence on bird communities is desirable. It may be calculated with the help of linear qualitative approximation with due regard for nonlinear changes of communities. To observe the degree of environmental factor's influence on the communities in the whole, but not on the separate species or the particular parameters of the communities, it is necessary at first to pass on the integral estimation of their heterogeneity. Such measure is the Jaccard's coefficient (Jaccard, 1902), calculated with due regard for the abundance of birds (Ravkin, 1973). This coefficient reflecte not only epeciee epecificity of communities, but the abundance of epecies, the degree of overlapping of their number in the comparing habitate, correlated with differencee in the same indices. The comparison of the degree of coincidence of communitiee's resamblance and the eame influence of the main environmental factore make it poseible to judge about the correlation between the heterogeneity of communitiee and environment. Including the anthropogenic influence (Ravkin, 1967, 1973).

To our regret we have no comparable data of bird's censuses in the towns of forest zone. The bird's communities of the urban habitats are investigated only in the villages. Multiple approximation of variability of avian communities in the kind of resemblance index'es matrix by the environmental factors fluctuates from 75 to 89% of dispersion. The most indices of the accounted dispersion are in the mounting-forest belts (89% in the first half of summer and 87 – in the second). The lesser part of variability is poesible to explane inside of separate subzones of forest zone in the plain (in the southern taiga of West Siberia correspondingly 87 and 83% and of the West and Middle Siberia – 80 and 77%). In the whole zone in the ranges of river Ob region the indices are lesser (80 and 75%). The approximation is effective enough when the separate numbers of display of environmental factors are used (for instance the high, middle and low woodness) as the separate subsidiary indications. Besides the such simple factors, their indivisible combinations (nature regimes) take part in approximation. They are formed by 17 comparatively simple factors. They are: woodness "macrowoodness", mosaic, regionality, faunal provinciality, absolute altitude under sea level, altitudinal zonality, subzonal alteration of climate, damping, composition of forest-making freeds, productivity and providing of phytocoenosises by mineral mitrition, "steppeness", dimension of swamp tracts, presence of reservoirs of high trophic, presence of yerniks and the anthropogenic influence –

building, forest felling, pasture of cattle, hay-making, ploughing, regulation of river flow.

The whole complex of anthropogenic factors in the forest – mountain belts of North-Eastern Altai (including secondary forest-steppe and the golets'es and pregolets's habitats) determinates 21-22% of dispersion of summer bird communities. In the forest zone of river Ob region this indices from 12% and just as many as in the southern taiga of West Siberia (10-12%) and in the same subzone in the West and Middle Siberia – 6 and 13% (in the I and II half of summer not accounting the town's ornitocomplexes).

The differences of indices are connected with the considerably greater ploughing in piedmonts of Altai and West Siberia in comparing with Middle Siberia. In average by the whole data the influence of anthropogenic transformation explains 14-15% of dispersion of summer bird's communities. The most important in this data is the influence of differences in woodness (43-46%) and some other factors, closely correlated with it ("macrowoodness", the forest type of landscape, the composition of forest-making breeds) and also productivity, and in the mountains-altitudinal zonality.

By the way, the most part of environmental signs are correlated with others, including anthropogenic influence and woodness because the first in the considerable degree determinate the second.

In the Ob valley within the limits of forest-steppe the pine forests and derivative communities are prevail over by their area. We may consider this territory as the part of the forest zone in the limits of forest-stepps. Here of the urban territories not only the settlements are investigated but also the Novosibirsk city. It permits to conduct the more complete estimation of the anthropogenic influence on avian communities. At the expense of sharp differences of bird's populations of town from the more or less natural communities anthropogenic influence explains here already 52-53% of territorial variability of communities. If we exclude the birds of the town from the calculations, the estimation decreases more than twice (20-22%). The relation with woodness of the territory form 21-28%, and after excluding of urban communities – 33-44%.

Novosibirsk is situated on the boundary of forest-steppe and podtaiga zones. Therefore it is possible to include the data of it's bird's population in the calculations of the forest's zone with some assumptions. The including of data of this ornitocomplexes in the forest zones and belts for the first half of the year by 2 years of our investigations increase the power of relation with anthropogenic influence to 35% (i.e. on 20%) and decreases the estimation of influence of woodness on 33% (i.e. on 10%).

Proceeding from this estimations we may suggest with confidence that in the limits of West Siberia the anthropogenic influence determinate the considerate part of territorial variability of bird's populations of forest zone, in any case, just the same with separate, the most significant natural factors of the environment. In the European part of the forest zone where the area of habitats, transformed by man, is just more, the influence of people's activity, apparently predominate among environmental factors.

SUMMARY

The results of bird censuses in 328 habitats of East-European and Siberian forest zone, including some habitats of secondary forest-steppe, were analysed. In northern locations (subzones) the replacement of coniferous forests by mixed stands (which follows selective cutting) or by secondarily overgrown extensive clearings and burns brings only insignificant change in the values of diversity, density, bird community biomass, and transformed energy indices. In southern locations such as southern parts of boreal region, secondary forest-steppe woods or forests, however, the values of these indices clearly increase when calculated for early stages of succession on clearings and burns, for mixed forests formed on older clearings and sometimes even partly ploughed areas. In such cases considerable changes in the species composition of predominating birds are also found.The construction of buildings leads to particularly pronounced increase in the summative community indices, except that of diversity, which essentially decreases. On the other hand, lower values of these indices were observed for the stages of small-leaved forests, for pasture degression and extensive fields. Generally, in northern regions the differences between primeval and secondary habitats cause smaller variations in index values than in southern ones.

Thus, anthropogenic transformations of forest bird communities is essential only in those cases when it is not within the frame - work of natural succession (forest maturation, pyrogenic succession or following the outbreak of pests), namely urbanization, pasture degression, extensive monocultural farming and construction of hydro-electric power stations.

When analyzing regional differences in bird fauna, only 15% of heterogeneity in bird community composition (expressed as coefficients of resemblance in quantitative traits) can be easily connected with anthropogenic changes. On the whole, under the multiple approximation, about 85% of dispersion of coefficients in resemblance matrices is possible to explain.

R e f e r e n c e s

Jaccard P. - Bull. Soc. Vaund. Sci. Nat.,1902, 38, p. 69-130.
Naumov R.L. Ptitsi v ochagakh klestchevogo enzefalita Krasnoyarskogo kraya.
    Avtoreferat dissertatsii kandidata biologicheskikh nauk.Moskva,1964.19 p.
Ravkin Yu.S. - In: Priroda ochagov klestchevogo enzefalita na Altaye. Novo-
    sibirsk: Nauka, 1967, p. 66-75.
Ravkin Yu.S. Ptitsi lesnoy zony Priobya. Novosibirsk: Nauka, 1973. 375 p.

# BIRDS AND MAN-MADE ENVIRONMENTAL CHANGES
# IN THE ARID ZONE OF THE USSR

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The problem "Birde in the man-made landscape" has been one of the central problems of ornithology within the last ten yeare. To-day it ie more than ever closely linked with the problem "Man and biosphere".

Man-made changee in landscapes are natural. They are determined by eociety neede ae well ae by the type of landscape and ecosyetem (Gladkov, Rustamov, 1965). In thie connection we can note, that typical and trophic chaine of arid ecoeyeteme, in comparison with other terreetrial ecoeyetems of the USSR, are simpler, and that ie why they are fragile and come rather easily under the influence of anthropogenic factore. Under thees circumetances greater thoughtfulneee and carefulneee are needed in utilizing arid areas and transforming their ecoeysteme. The USSR zone of deserte stretchse from the shoree of the Caepian Sea to the weet up to the Djungar Ala Tau, Tien Shan and the Pamire-Alai to the east and eouth-eaet. The eouthern boundary passee along the Kopetdag and Paropamis foothills. To the eaet of the Caspian Sea there are deeert areas in the Eastern Caucasue. The main desert landscapee are eituated in Central Aeia and Kazakhetan, their total area making up about 230 million ha. Deserte are diverce: clayey, detritue and sandy. They differ in their ecoeyetems and fauna.

The avifauna of the USSR arid zone includes 300 epeciee and eubepecies. 60 to 65 of them are neeting and settled birds, the reet etay in the deserts temporarily (migrating, wintering and casually flying by birds). They are intrazonal. Typical desert epeciee form no more than half of the neet fauna. They are: Pterocles orientalie, Pt. alchata, Chlamydotis undulata, Cureorius cursor, Burhinus oedichemue, Charadrius leschenaultii, Ch. aeiaticus, Caprimulgus aegyptiue, Dendrocopoe májor, Oenanthe deeerti, O.isabellina, Scotocerca inquieta, Sylvia curruca, S.nana, Hippolaie·rama, Hippolaie languida, Galerida crietata, Paeeer simplex, P.ammodendri, Podocee panderi and othere. Ecological and genealogical linke of theee epeciee with the desert are deep and etable. They poseese a number of morphophyeiological and adaptive featuree and adaptive behavior methods allowing them to exiet under extreme conditione. In the proceee of evolution theee forms have succeeded in gaining and coneolidating exceptionally important adaptive features, i.e. economical water intake and the ability to retain it in the organizm ( Ruetamov, 1954).

Man-made environmental changee almoet alwaye tell negatively on typical desert birde, but the eame changee tell positively on ecologically plaetic (intrazonal) epeciee. It ie well-known, for example, that irrigation, the opening up of virgin lands and ploughing, deetruction of buehee has led to the narrowing of the range, the reduction of the eize, the eplitting up of the population and the vanishing from theee areae of many typical deeert epeciee, in particular - Pteroclee orientalie, Chlamydotie undulata, Cureoriue cursor, Charadrius aeiaticue, Ch.leschenaultii, Sylvia nana, Paeeer simplex, Podocee panderi. The appearance and neeting on irrigated and developed areae of the deeert of Columba livia, Streptopelia eenegaleneis,Upupa

spops, _Acridotheres tristis_, _Passer domesticus_, _P.montanus_ and others testifies to the "florishing" of the ecologically plastic species.

The composition, distribution and size of the bird population change according to the period of time (duration) and intensity (degree) of the influence exercised by man and his activities on the landscape and its fauna (Drozdov, 1967). Time is of course an important factor, but much depends on the intensity of the anthropogenic pressure. Thus, for example, the avifauna of the oasis in the centre of the Repetek biosphere reserve has, in comparison with other areas of the Eastern Karakums, a more "cultivated" character (_Accipiter badius_, _Athene noctua_, _Upupa epops_, _Columba livia_, _Acridotheres tristis_, _Passer domesticus_, _P.montanus_, _Rhodospiza obsoleta_ and others), acquired within the period of the past 80-110 years. In all 45 species and subspecies of birds, including 9 nesting ones, were registered in the Repetek reserve anthropogenic areas. In summer the size of the bird population in the anthropogenic biotopes of the reserve makes up 3896.3 individuals per 1 sq km, while in the habitats, which were not transformed, there are from 26.9 to 300.3 individuals per 1 sq km.

The comparison with the avifauna, which developed during the past 20-25 years on some areas of the Karakum canal, shows that the Repetek oasis fauna is noticeably poorer. The bird fauna of the Karakum canal includes more than 200 species and suspecies of birds, including about 80 nesting ones. And there is another example: in spring in the Karakum desert in the regions of very poor development 22 individuals fall on 1 sq km, 70 and 31 individuals fall on 1 sq km in noticeably transformed ecosystems and 100 and 90 – in very transformed ones (oases). That is the result of irrigation.

Water is a powerful factor in the transformation of desert ecosystem.

The penetration of man into the desert began with the discovery of water. People learned to dig wells and kyarizes and to construct sardobas. A kyariz is a remarkable irrigation construction, with its aid fresh underground waters are brought from the foothill to the desert valley. A sardoba, on the other hand, serves as a reservoir for collecting winter and spring precipitation. These irrigation constructions are far removed from each other. Near them man settles with his cattle and there appear spots of crop areas. This initial impact of man on the desert which is connected with the appearance of water slightly improves birds living conditions and among some of birds there arise contacts with water and other elements of man-made landscape (Rustamov, 1956).

The ornithogeographical significance of these contacts lies in the fact, that it is quite often from these contacts the species begin to habite near man. Subsequently, the transformation of the temporary contacts into constant ones is not obligatory. It is quite another thing, when canals and reservoirs are constructed, broad irrigation networks, supplying fields with water appear, settlements, orchads, field-protecting shelterbelts are layed out. All that has a great anthropogenic influence on the desert. It is caused by large-scale irrigation of arid areas. As a result of that ranges become wider or narrower, new relations within the ecosystems arise, birds mode of life and behaviour change to a great extent. All that takes place under the in-

fluence of irrigation and water conveyance, indirect anthropogenic influence upon birds through the change of their places of habitation (Rustamov, 1930).

Natural arid ecosystems are rather unproductive. The coming of an abundance of water to the desert raises the feeding capacity of transformed lands, increases productivity of the ecosystems and satisfies water requirements of birds. Favourable ecological conditions spread to vast areas and serve as a kind of a gutter, through which birds (from already formed anthropogenic ecosystems) settle on developed lands. Thus birds habitating on the Amudarya, Murgab, Tedjen rivers and on the intrazonal complexes of adjacent deserts practically besiege settlements and cultivated areas along the Karakum canal. Cultivated lands expand, and following that a marked intra-range settling of different bird species takes place (Rustamov, 1976). Ornithogeographically this settling occurs mainly thanks to species brought from river valleys and only partly taken from undeveloped desert areas. Such a picture may be observed not only with birds, but with other groups of animals, including insects, fishes, amphibia, reptiles and mammals.

Consequently, agricultural desert reclamation, relying on broad irrigation development, possesses an important ecological characteristic of continuity, which at the same time is important for ornithogeography, as it is conductive to intra-ranged bird settling.

Intra-ranged settling is the settling of birds within the range of the ever widening area of the biotopes, which answer the requirements of the species. The appearance of Columba livia, Passer montanus, P.domesticus and others on the irrigated areas is an example of intra-range settling of certain species. When in connection with favourable ecological conditions the corresponding groups of bird species (Ardea cinerea, Botaurus stellaris, Nycticorax nycticorax, Himantopus himantopus, Vanellachettusia leucura, Charadrius dubius, Pica pica, Sturnus vulgaris, Motacilla flava, Emberiza bruniceps, Hirundo rustica, Riparia riparia and others) move from river valleys of East Turkmenia onto the Karakum canal, then we speak about large-scale intra-range bird settling. Birds of this group on the Karakum canal make up from 40 to 60% of nesting species (Belskaya, 1967). As is generally known, when birds settle for good, the range of the species widens. For example, Acridotheres tristis nests in a number of places of the Karakum canal.

The irrigation of arid lands considerably influenced bird settling during their migration and wintering. In favourable years 500-600 thousand ducks, coots, geese and other waterfowl winter on all artificial reservoirs, that makes up 10% of all birds, concentrating on large winterings of the USSR. Such mass winterings developed during the past 20-25 years. Lakes with drain water are less favourable and the number of wintering birds is insignificant. Reservoirs that appeared on arid lands attract many birds during their spring and autumn flights. "Broad front" migration, which is quite usual for bird movement in the desert, abates and is replaced by relatively narrow flight ways along artificial lakes (Rustamov, 1976).

Water in some places of the desert radically changes the appearance of the ecosystem and its fauna. Before the formation of the large reservoir in the Sarykamysh hollow, 20 bird species in all habitated there. These were mainly desert species (Rustamov, 1948). When in the beginning of the 60-ies

drainage waters were thrown from irrigated fields into the hollow, a saltish-water reservoir appeared, stretching from the north to the south for a length of 130 km and from the west to the east - 60 km. In 1975-1976 84 bird species, including 24 nesting ones, were observed at the Sarykamysh reservoir. Bird species habitating on water and near water dominate in the fauna of the reservoir. Thus the total number of Pelecanus crispus on the investigated area of the reservoir reached 1 thousand species, Fulica atra - 600 species, Phalacrocorax carbo - 1.5 thousand species and about 250 nests of Hydroprogne caspia were found there (Velikanov, Khokhlov, 1979).

Up to now we have spoken about the indirect impact through irrigation and water conveyance on birds, as one of the components of arid ecosystems. This impact is the result of other economic activities of man, such as exploring of minerals, constructing of oil- and gas-pipes, a railway and motor-roads, etc. It has been established, for example, that the building of the railway in the sandy lands of the North-East Karakums near the Caspian Sea, led to a sharp change in the composition of bird fauna. The number of nesting species has increased one and a half times, mainly by burrow, rock and synanthropic species not to be found in undisturbed by man sandy lands. The composition of the fauna has become more diverse and less specific for the sandy desert. At the same time the general density of the bird population has been reduced more than two times.

The formation of favourable to man ornithologic complexes in the desert has unfortunately been going on and is still going on spontaneously. This process can't even be called controlled. To avoid this, ornithologists should at least participate in the planning of the large-scale alterations of the arid ecosystems (Rustamov, 1980).

References

Belskaya G.S. - In: Ptisi kulturnogo landshafta. Ashkhabad, 1967, p. 9-16.
Velikanov V.P., Khokhlov A.N. - In: Prirodnaya sreda i ptisi poberezhiy Kaspiiskogo morya i prilezhastchikh nizmennostey. Baku, 1979, p. 236-240.
Gladkov N.A., Rustamov A.K. - In: Sovremennye problemy ornitologii. Frunze, 1965, p. 111-156.
Drozdov N.N. - In: Ornitologia. Moscow, 1967, vyp. 8, p. 3-46.
Rustamov A.K. - Doklady AN SSSR, 1949, vol. LX, N 8, p. 1449-1451.
Rustamov A.K. - Tr. Turkm. selkhosinstituta (Ashkhabad), 1956, vol. VIII, p. 279-291.
Rustamov A.K. - Problemy osvoenia pustyn, 1969, N 2, p. 9-14.
Rustamov A.K. - In: Teoreticheskie i prikladnye aspekty okhrany prirody i okhotovedenia. Vol. 84. Moskva, 1976, p. 40-44.
Rustamov A.K. - In: Ekologia, geografia i okhrana ptits. Leningrad, 1980, p. 138-143.
Rustamov A.K.-In: Acta Congr. Int. Orn.,1954. Basel, 1955, p. 510-515.

# CHANGES IN THE BREEDING AVIFAUNA OF AGRICULTURAL LAND IN LOWLAND BRITAIN

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## INTRODUCTION

The agricultural landscape of lowland Britain is among the most drastically altered by man. 2,000 years ago the lowlands were clothed in broad-leaved forest interspersed with marshes. Gradually the change from forest to an agricultural landscape took place until today 80% of the land use in Britain is agricultural and only 8% remains forested. It is difficult to establish the gains and losses of the avifauna during this long transition. Certainly the drainage of the once extensive tracts of marsh helped towards the extinction of such speices as Crane Grus grus, Spoonbill Platalea leucorodia, Bittern Botaurus stellaris and Black Tern Chlidonias niger. It is also clear that the opening up of the forests allowed the colonisation of scrub and open country species of birds into this much diversified habitat, but the majority of British farmland species are those with a woodland origin - the dominant species being Blackbird Turdus merula, Dunnock Prunella modularis, Skylark Alauda arvensis, Robin Erithacus rubecula and Chaffinch Fringilla coelebs (Williamson, 1967).

After the development of the open field system of the Anglo-Saxons the agricultural landscape of lowland Britain remained relatively unchanged for a long period. The modern day landscape of a mosaic of fields, often bounded by hedgrows, with a patchwork of small pieces of woodland, ponds and farmsteads is largely due to the Enclosure period 1750-1850.

In this review of changes in the breeding avifauna of agricultural land in lowland Britain I shall consider the causes of change due to man's farming activities as well as changes due to natural phenomena such as climate, population pressure and range expansion and contraction. Much of the information comes from the British Trust for Ornithology's population monitoring surveys, the Common Birds Census, Waterways Bird Survey and Nest Records Scheme, although information has been included from other sources where appropriate.

## CHANGES IN THE AVIFAUNA IN RELATION TO AGRICULTURAL CHANGE

Following the Industrial Revolution of the 18th century an expansion of farming to a commercial industry took place resulting from the steep rise in human population. New technology led to an increase in mechanisation and one of the first species to suffer was the Corncrake Crex crex. A decline was first noticed in the second half of the 19th century in the areas of greatest cultivation in south east England. The mechanical cutting of hay allowed mowing to take place progressively earlier, so destroying adult birds, nests and small young. The decline still continues with the species all but extinct as a breeding species in England and Wales with a reduction in occupied 10 km squares between 1968-1972 and 1978-1979 of 95% in England and Wales and 56% in Scotland. The major strongholds are now in the west of Scotland, especially the islands, where the small meadows with the adjoining marshes are still farmed by traditional methods and are not cut until late July (Cadbury,1980).

Since 1945 agriculture has greatly intensified due to modern technology and also encroached more and more on other habitats.

HABITAT LOSS

Among the habitats most affected by agricultural expansion since the 1940s are lowland heath and chalk grassland, valuable for their specialised bird communities (Fuller, 1982). The losses have been considerable. For example, between 1811 and 1960, 40% of Dorset heathland was lost while during 1960 to 1978 a further 40% was eroded (Stubbs, 1980), mostly ploughed up for arable farmland. The conversion of so much heath and grassland, together with a reduction in grazing on the remainder, due to myxomatosis affecting the rabbit Oryctolagus cuniculus population from 1954, has had a locally deleterious effect on populations of grassland species in southern England such as the Wheatear Oenanthe oenanthe and Stone Curlew Burhinus oedicnemis. For example, both are now almost extinct as breeding species in Sussex, southern England, whereas in 1938 they were relatively abundant (Shrubb, 1979). This is also true for many other areas in lowland Britain. In fact the majority of pairs of Stone Curlews in Britain are now to be found breeding on arable farmland where they are subject to much greater disturbance and suffer higher losses of eggs and young due to farming activities (Glue, Morgan, 1974).

Another major form of habitat loss on farmland is caused by increased drainage. The rate of drainage improvement of arable famland and also of flood-meadows and grazing marshes has risen steeply since 1945 - from 12,000 hectares per year to over 100,000 hectares per year at present (Williams, 1982). There has been an estimated 30% reduction in the area of old pasture in Britain since 1940 (Moore, 1962). This has led to the decline of many populations of breeding waders, particularly Redshank Tringa totanus, Snipe Gallinago gallinago and Lapwing Vanellus vanellus. In many midland and southern countries of England there has been a widespread decrease in Snipe due to improved drainage (Parslow, 1973) and the population index from the Common Birds Census and Waterways Bird Survey shows an 18% decrease between 1974 and 1978 (Marchant, Hyde, 1978). In Sussex, southern England the Snipe population had decreased from 500 pairs in 1938 to less than 100 pairs in 1967 and for Redshank from 400 pairs to 250 pairs in the same period (Shrubb, 1979). The Common Birds Census population index also shows a decline for Lapwing in the south and east of Britain but not in the north and west (Marchant, pers.comm.).

To facilitate improved drainage many rivers and streams in lowland Britain have undergone drastic changes in the form of widening and straightening the channels and regrading the stream bed, usually involving the felling of bank-side tress and scrub (Smith, 1975). This represents a large loss of habitat for many specialised riparian species. At present the British Trust for Ornithology and the Royal Society for the Protection of Birds are gathering information on the bird populations of managed and unmanaged stretches of rivers, in some instances on the same sections before and after management by the Water Authorities, to assess the initial impact and subsequent changes in bird communities. For example, censuses carried out on a farm in Dorset southern England, showed populations of between 21 and 29 pairs of 7 breeding riverside species in each of three years before dredging and bank clearance operations took place but only 12 pairs were present three years afterwards

(Williamson, 1971). The species most affected were the Reed Warbler <u>Acroce-phalus scirpaceus</u> and Sedge Warbler <u>Acrocephalus schoenobaenus</u>, the latter showing a movement away from the river to breed along hedgerow ditches. Moor-hens <u>Gallinula chloropus</u> can also be greatly affected by dredging as shown by an example from the Waterways Bird Survey where the numbers were reduced from five to one following management work (Marchant, Hyde, 1980).

HEDGEROWS

One of the most obvious changes in the farmland landscape of Britain is the loss of hedgerows - 23% (225,260 km) since 1945 (Stubbs, 1980). There has been much controversy over the value of hedges to wildlife - on the one hand the farmer wishing to make the running of the farm as efficient as possible and the conservationist on the other hand seeing all habitat loss as detri-mental for wildlife.

Hedgerows provide nest sites, food and shelter for birds and are more im-portant for some species than others.The size,shape and management of hedges greatly affects their value to nesting birds (Moore et al., 1967) and there-fore some hedgerow loss, particularly of poorer quality hedges, will not ne-cessarily lead to a significant reduction in the numbers of birds on the farm farm (Murton,Westwood,1974; Bull et al.,1976).However,a comparison of the open field system of farming with virtually no hedgerow with nearby enclosed land showed a three-fold increase in the number of birds when the hedge nesting species were included (Moore et al., 1967). A Common Birds Census carried out on a Cambridgeshire farm in eastern England from 1964-71 showed that a loss of 95% of hedgerows led to a 49% loss of species nesting in hedgerow, tree and thicket (Evans, 1971). Some species were not affected by this hedgerow loss and even increased, for example Skylark and Reed Bunting <u>Emberiza schoeniclus</u>. Hedgerows are known to be important components of the farmland habitat for Yellowhammers <u>Emberiza citrinella</u>. Studies on the effect of severe cut-back of hedgerows on farmland in Hertfordshire, southern England, showed that the Yellowhammer responded to this loss of habitat quality by greatly expanding its territory size (Morgan, O'Connor, 1980), perhaps in order to obtain suf-ficient food. On the same farm the Dunnock <u>Prunella modularis</u> responded by shifting territories from the cut-back internal hedgerows to the previously less preferred boundary hedges remaining. Although the relationship between birds and hedgerows is as yet poorly known, it is already clear that for some species they are of major importance: among the farmland species monitored by the Common Birds Census 37% of the species are positively correlated with hedgerows with trees and 30% with hedgerow density, a much greater proportion than with variables such as area of woodland, scrub and lines of trees (O'Con-nor,in prep.).

A factor contributing to hedgerow loss is the infection of elm trees <u>Ulmus</u> spp. with Dutch elm disease. Between 1969 and 1978 out of a total of 17.1 mil-lion elms, 10.6 million were dead or dying and 5 million had been felled.From a study using Nest Record Scheme data the loss of elms was considered to have caused a large reduction in the available nest sites for Kestrel <u>Falco tin-nunculus</u>, Tawny Owl <u>Strix aluco</u>, Stock Dove <u>Columba oenas</u> and, in particular, Barn Owl <u>Tyto alba</u> (Osborne, 1982). Some species, notably Woodpeckers (<u>Pi-cidae</u>) and Nuthatch <u>Sitta europaea</u> may have benefitted from the temporary

abundance of beetle larvae on dead elms, but Chiffchaffs <u>Phylloscopus col-</u><u>lybita</u> have also declined on those Common Birds Census plots affected by Dutch elm disease compared with unaffected plots (Osborne,in prep.).

PESTICIDES

The possible effects of pesticides on farmland bird populations first came to light during the 1950s when granivorous birds were being killed in large numbers during seed-dressing incidents and the bodies were found to contain very high levels of organo-chlorine insecticides (Prestt, Ratcliffe, 1972). However, there is no evidence of permanent effects on populations of these species but spectacular declines have been seen in various predatory species throughout Britain such as Peregrine <u>Falco peregrinus</u> and Sparrowhawk <u>Acci-</u><u>piter nisus</u>.

The introduction of DDT as a seed-dressing since 1947 and the more toxic cyclodiene compounds of aldrin, dieldrin and heptachlor since 1956 were coincident with egg-shell thinning, egg-breakage and poor breeding success in Sparrowhawks, such that a marked population decline occurred over much of south, east and central England, particularly in intensive arable areas (Newton, 1973). Sparrowhawk populations breeding away from arable land did not show this poor breeding success,and in these areas organochlorine pesticides were never widely used (Newton, 1974). The situation is healthier now following restrictions on the use of these chemicals and the Sparrowhawk is once more frequently seen hunting over farmland areas. Since the inception of the Common Birds Census in 1962 the percentage of farmland and woodland plots recording  Sparrowhawks has steadily increased (Marchant, 1980).

Another species that showed a large scale population decline in the 1950s, particularly on arable farmland, was the Stock Dove (Parslow, 1973). A recent study using nest record card data has shown that breeding success was much lower in the period 1950-69 than in the preceding or succeeding decades, thus coinciding with the main period of organochlorine pesticide usage (O'Connor, Mead, 1981).

Another group of chemicals that have affected birdlife in lowland farmland areas in Britain are herbicides. Herbicide use on cereals dates back to the beginning of the century but was not extensive until the 1960s. Between 1969 and 1977 the annual acreage sprayed with herbicides has increased by 25% (Stubbs, 1980). The effect of spraying is to reduce the dicotyledenous weed flora which in turn reduces the arthropod biomass in the fields. A single application of certain herbicides to a cereal field in April will, by June, have reduced the arthropod biomass by two-thirds compared with an unsprayed control field (Southwood, Cross, 1969).

Grey Partridges <u>Perdix perdix</u> have been declining in Britain since the 1950s due to a change in chick survival. This has been caused largely by the reduction in arthropod food through the increased application of herbicides making the chicks more dependent on aphids as food. This renders the chicks very susceptible to spring temperature as the aphids move into cereal fields much later in cold springs (Potts, 1970).

The Common Birds Census index for the Linnent <u>Acanthis cannabina</u> also shows a decline from 1962-81 and this species is very dependent on the weeds of cultivation (Newton, 1972). Perhaps herbicides are again responsible.

## OTHER FACTORS AFFECTING CHANGE IN THE BREEDING AVIFAUNA

Changes in the breeding avifauna can be caused by other, natural factors such as climate, population pressure and range expansion or contraction independent of changes in agricultural practices.

### CHANGES IN WINTER SURVIVAL

Small, resident species such as the Wren Troglodytes troglodytes, Long-tailed Tit Aegithalos caudatus and Treecreeper Certhia familiaris were particularly reduced in numbers in the two severe winters monitored by the Common Birds Census in 1962-63 and 1978-79. Larger species were not affected so badly. Also, the survival of species wintering in parts of West Africa, subject to severe drought conditions between 1968 and 1969, were much reduced; by up to 75% in the case of Whitethroat Sylvia communis (Winstanley et al., 1974). Other farmland species showing declines correlated with the Sahelian drought include Sedge Warbler, Garden Warbler Sylvia borin, Spotted Flycatcher Muscicapa striata and Swallow Hirundo rustica (Marchant, 1982).

### FARMLAND AS A SUBOPTIMAL HABITAT

The habitat preferences of a particular species may be influenced by these large scale changes in population levels. For instance following the 1962-63 cold winter the majority of Wren territories were concentrated in to woodland and streamside habitats and as these habitats became saturated with the increase in population level, gardens and finally farmland hedgerows were occupied (Williamson, 1969). Farmland is therefore a suboptimal habitat for the Wren and this has also been shown for the Great Tit Parus major (Krebs, 1971) and the Woodpigeon Columba palumbus (Murton, Westwood, 1974).

### RANGE EXPANSION AND CONTRACTION

Finally, let us consider changes due to range contraction or expansion. Britain is on the edge of the range for a number of species and is therefore likely to be more affected by population changes than the centre of the range. The Red-backed Shrike Lanius collurio is an example of a scrub and hedgerow species in severe decline in Britain since the 1950s. The population had declined from 253 pairs in 1960 to 81 pairs in 1971; a drop of 68% (Bibby, 1973). At the same time one of the most dramatic examples of range expansion occurred in the Collared Dove Streptopelia decaocto from Asia across Europe to reach Britain in 1955. This species now breeds over most of the country and has graduated from being specially protected to being a farmland pest (Sharrock, 1976).

R e f e r e n c e s

Bibby C. - Bird Study, 1973, 20, p. 103-110.
Bull A.L., Mead C.J., Williamson K. - Bird Study, 1976, 23, p. 163-182.
Cadbury C.J. - Bird Study, 1980, 27, p. 203-218.
Evans P.J. - Cambridge Bird Club Report, 1971, 1972, 45, p. 36-39.
Fuller R.J. Bird habitats in Britain. Calton, Poyser, 1982.
Glue D.E., Morgan R.A. - Bird Study, 1974, 21, p. 21-28.
Krebs J.R. - Ecology, 1971, 52, p. 2-22.
Marchant J.H. - Bird Study, 1980, 27, p. 152-154.
Marchant J.H. - Bird Study, 1982, 29, p. 143-148.
Moore N.W. - Brit. Birds, 1962, 55, p. 428-436.
Moore N.W., Hooper M.D., Davis B.N.K. - J. Appl. Ecol., 1967, 4, p. 201-220.
Morgan R.A., O'Connor R.J. - Bird Study, 1980, 27, p. 155-162.
Murton R.K., Westwood N.J. - Brit. Birds, 1974, 67, p. 41-69.
Newton I. Finches. L.: Collins, 1972.
Newton I. - Brit. Birds, 1973, 66, p. 271-278.
Newton I. - J. Appl. Ecol., 1974, 11, p. 95-102.
O'Connor R.J., Mead C.J. Population level and nesting biology of the Stock
    Dove Columba oenas in Great Britain, 1930-1980. Report to the United
    Kingdom Nature Conservancy Council. 1981, p. 1-47.
Osborne P. - Bird Study, 1982, 29, p. 2-16.
Potts G.R. - Bird Study, 1970, 17, p. 145-166.
Prestt I., Ratcliffe D.A. Effects of organochlorine insecticides on
    European birdlife. Proc. Int. Orn. Congr. 15, 1972, p. 486-513.
Sharrock J.T.R. The Atlas of Breeding Birds in Britain and Ireland. Calton.
    Poyser, 1976.
Shrubb M. The birds of Sussex, their present status. Chichester. Phillimore,
    1979.
Smith A.E. - Bird Study, 1975, 22, p. 249-254.
Southwood T.R.E., Cross D.J. - J. Anim. Ecol., 1969, 38, p. 497-509.
Stubbs A.E. Nature Conservancy Council Chief Scientist's Team. Notes N 21.
Williams G. - BTO News, 1982, 119.
Williamson K. - Bird Study, 1967, 14, p. 210-226.
Williamson K. - Bird Study, 1969, 16, p. 53-59.
Williamson K. - Bird Study, 1971, 18, p. 80-96.
Winstanley D., Spencer R., Williamson K. - Bird Study, 1974, 21, p. 1-14.

# MEDITERRANEAN BIRD FAUNAS IN THE LIGHT OF ANTHROPIC PRESSURE SINCE THE NEOLITHIC

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## THE BIRD FAUNAS OF THE MEDITERRANEAN AREA BEFORE THE IMPACT OF MAN

Any attempt to describe the influence of human activities on bird faunas needs first to know what was the pattern of the distribution of species and communities before the impact of man began to be apparent on the landscape. Needless to say that such a task is hazardous and speculative but several cues help us to know something about the nature of the avifaunas during the Atlantic period (7500 - 4500 BP), that is just before the intervention of neolithic man on a large scale starts to be apparent in pollinic diagrams (Pons, 1981; Pons, Quézel, 1981). An examination of the biogeographic affinities of the 209 land birds out of the 335 species breeding in the Mediterranean basin shows that they belong to three main faunal categories (Blondel, 1982): 1) boreal sylvatic species widespread in both deciduous and mixed forests of the Palearctic = 74 species, 2) birds of Palearctic grasslands and of southern and south-eastern steppes = 92 species, 3) birds of mediterranean type shrublands = 43 species. A first conclusion which merges from these figures is the importance of birds of boreal sylvatic origin. Palaeobotanical studies show that at the maximum of development of forest vegetation during the Atlantic period, forests were widespread in many forms everywhere in the mediterranean area (Beug, 1967; Triat-Laval, 1978; Pons, Quézel, 1981). Many indications, both palaeobotanical and paleontological (Mourer-Chauviré, 1975; Blondel in press) suggest that the bird faunas of these climactic forests of the mediterranean basin were not markedly different from those of temperate deciduous and conifer forests further north. So, the largest part of bird communities of the Mediterranean were dominated either by boreal forest species in the deciduous lowland and conifer montane forests or by freshwater birds (70 species = 21% of the total) in marshes, rivers and lakes. Such a situation is an inheritance of glacial times when the forest avifaunas of Europe could survive only in the mediterranean basin (Moreau, 1954). These avifaunas expanded to the north during post-glacial times as they probably did during each interglacial period since the beginning of the Pleistocene, but their composition remained roughly the same within the mediterranean basin in the interglacial time as the one at the present time, until the beginning of human pressure. Nevertheless it must be emphasized that the great topographical and geobotanical diversity of the Mediterranean always allowed besides the medioeuropean avifaunas the existence of truly mediterranean species and species of steppes in the mosaic of habitats which exists in the region since the beginning of the Pleistocene. On average, the steppic and semi-arid species which evolved in the xeric habitats encircling the Mediterranean from the shores of the Atlantic ocean to the steppes of Central Asia (for example Larks, Chats, Sandgrouses) had by these times a more southern distribution than now as will be shown later.

As far as the mediterranean species are concerned, it was shown elsewhere

'in this Congress (Blondel in press) that some speciation took place during
the Pleistocene within the present mediterranean area, especially for bush
species such as Sylvia spp., Hippolais spp., Alectoris spp. and some others.
For these species as well as for other bush species of more northern origin,
it must be recognized that some shrubland-like habitats must always have
been present since the beginning of glacial times, which is confirmed by pa-
leobotanists (Suc, 1973; Vernet, 1972). This is not surprising given the
great physiographic diversity of the region. Botanists have shown that since
the setting up of a truly mediterranean bioclimate by the end of the Pliocene,
some kind of matorrals (maquis, garrigues, phrygana) dominated by a truly me-
diterranean vegetation have always been present, even during the most severe
phases of the last glaciation, but at a much lower geographical scale than
now and under the form of local patches. Hence the small number of bush spe-
cies such as Sylvia which evolved locally in contrast with the dominance of
temperate forest species which made up the great bulk of land birds.

THE CONSEQUENCES OF HUMAN ACTIVITIES ON MEDITERRANEAN BIRD
COMMUNITIES: INDIRECT EVIDENCE

The bird communities of climactic mediterranean forests

The mediterranean habitats have been under human pressure for 4000 to 6000
years according to the places. This strong pressure results everywhere in the
reduction of forests and the extension of matorrals. Our minds are so much
impregnated by the modern landscapes that it is difficult to imagine that
most matorrals are secondary formations which took the place of former fo-
rests. Since my experience is mostly from southern France, I shall mainly
deal with the bird communities of this region.

One of the most puzzling facts that the ornithologist can notice is that
the bird communities which live in the few relictual patches of old forests
which are near a climactic state have no mediterranean character. How to ex-
plain such an apparent paradox? The comparison of the bird communities of
four old forests, two of them in central France (Burgundy and Fontainebleau
near Paris) and the two remaining in mediterranean France (Provence and Cor-
sica) shows that on average the composition of these four communities is
quite similar (Table 1). There is less species in Provence and especially in
Corsica because of island effect (Blondel, 1979, 1981). Only five species
were found in the mediterranean forests. Actually, three of them (Luscinia
megarhynchos, Phylloscopus bonelli and Parus cristatus) breed in the surroun-
dings of the temperate forests which were censussed, Certhia familiaris in
Corsica is replaced on the mainland by Certhia brachydactyla and Serinus cit-
rinella is a species of the southern Alps which has important populations
everywhere in Corsica. On the other hand, 17 species (Columba oenas, Picus
canus, Dryocopus martius, Picoides medius, Jynx torquilla, Anthus trivialis,
Prunella modularis, Phoenicurus phoenicurus, Turdus philomelos, Phylloscopus
trochilus, Phylloscopus sibilatrix, Muscicapa hypoleuca, Parus palustris,
Parus montanus, Pyrrhula pyrrhula, Coccothraustes coccothraustes, Sturnus vul-
garis) which breed in the temperate forests are absent from the two mediter-
ranean ones but the mediterranean area is out of the range of most of them
and only Columba oenas, Phoenicurus phoenicurus, Coccothraustes coccothraustes

Table 1. Composition (numbers of breeding pairs per 10 ha) of bird communities in four old forests, two in central France (Burgundy, Ferry, Frochot, 1970; Fontainebleau, Le Louarn, Spitz, 1978) and two in mediterranean France (Provence, Corsica, Blondel, 1979). + = density less than .1 breeding pair

| Region | Burgundy | Fontainebleau | Provence | Corsica |
|---|---|---|---|---|
| Dominant tree | *Quercus pedunculata* | *Fagus silvatica* | *Quercus ilex* | *Quercus ilex* |
| *Columba oenas* | + | + | | |
| *Columba palumbus* | + | + | .1 | .1 |
| *Cuculus canorus* | | + | .3 | .1 |
| *Picus viridis* | .1 | .1 | .3 | |
| *Picus canus* | .1 | + | | |
| *Dryocopus martius* | | + | | |
| *Picoides major* | .7 | .1 | 1.8 | 1.1 |
| *Picoides minor* | .3 | + | .3 | |
| *Picoides medius* | 1.0 | + | | |
| *Jynx torquilla* | | + | | |
| *Anthus trivialis* | | 1.5 | | |
| *Troglodytes troglod.* | 2.3 | 14.5 | 5.0 | 5.0 |
| *Prunella modularis* | | 2.2 | | |
| *Phoenicurus phoenic.* | .8 | 2.3 | | |
| *Erithacus rubecula* | 2.9 | 9.2 | 6.1 | 5.7 |
| *Luscinia megarhynch.* | | | 1.4 | |
| *Turdus merula* | 1.0 | .1 | 3.8 | 1.1 |
| *Turdus philomelos* | 1.1 | .1 | | |
| *Turdus viscivorus* | .3 | | .2 | |
| *Sylvia atricapilla* | .5 | 4.2 | 5.5 | 6.7 |
| *Phylloscopus trochilus* | + | | | |
| *Phylloscopus collybita* | .4 | 7.4 | .8 | |
| *Phylloscopus bonelli* | | | 1.1 | |
| *Phylloscopus sibilatrix* | 3.6 | 6.1 | | |
| *Regulus ignicapillus* | | 1.8 | 1.5 | 9.0 |
| *Ficedula hypoleuca* | | 2.8 | | |
| *Muscicapa striata* | .2 | | | 1.8 |
| *Aegithalos caudatus* | .4 | .5 | | 1.0 |
| *Parus palustris* | 2.4 | 3.7 | | |
| *Parus montanus* | .2 | | | |
| *Parus cristatus* | | | 3.2 | |
| *Parus ater* | | .5 | .2 | 4.1 |
| *Parus caeruleus* | 12.6 | 14.1 | 11.6 | 14.1 |
| *Parus major* | 4.7 | 14.5 | 3.2 | 4.7 |
| *Sitta europaea* | 3.8 | 4.1 | 2.2 | |
| *Certhia familiaris* | | | | 1.6 |
| *Certhia brachydactyla* | 5.6 | 2.5 | 6.9 | |
| *Fringilla coelebs* | 5.6 | 4.4 | 7.7 | 6.4 |
| *Pyrrhula pyrrhula* | | 2.0 | | |
| *Cocc. coccothraustes* | .6 | 1.5 | | |
| *Sturnus vulgaris* | 3.9 | | | |
| *Oriolus oriolus* | .1 | | .1 | |
| *Garrulus glandarius* | .8 | .1 | .6 | 1.0 |
| *Serinus citrinella* | | | | .4 |
| Number of species | 30 | 33 | 23 | 17 |

and Sturnus vulgaris can be found in some mediterranean habitats. We have cal-
culated an index of similarity (beta-diversity using Shannon's formula) bet-
ween the four communities taken two by two (Table 2). As expected, the pairs
of communities which are geographically the nearest are more similar between
them than with the others but one must notice that the Quercus ilex forest of
Provence is very similar with the Quercus pedunculata forest of Burgundy. The
differences with the corsican forest are more a result of species impoverish-
ment due to insular isolation than of some biogeographical trend because only
two species, Certhia familiaris and Serinus citrinella are particular to the
island forest. We can conclude from these comparisons that the differences
between the bird communities of the mediterranean climactic forests and those
of the temperate forests are only differences in richness. This impoverishment
is perceptible in Provence but is much more pronounced in the corsical forest;
it must be related to the position of the region at the southern margin of
Eurasia (Blondel, 1979, 1981).

T a b l e  2. Indices of similarity of the bird communities of the four
forests taken two by two. Figures are $\beta$-diversities using Shannon's
formula $(H'_\beta = H'_{\alpha ij} - .5(H'_{\alpha i} + H'_{\alpha j}))$
B = Burgundy, F = Fontainebleau, P = Provence, C = Corsica

|   | B | F | P |
|---|---|---|---|
| F | .79 | − | |
| P | .75 | .71 | − |
| C | .63 | .64 | .78 |

## The dynamics of bird communities along ecological successions

The impact of man on the mediterranean vegetation and the degradation of
habitats can be illustrated by a gradient of decreasing complexity of vegetat-
ion from an old forest (right of **Fig.** 1) to a steppe (left of fig. 1). This
can be considered as an oversimplified generalisation of the consequences of
human activities on mediterranean vegetation. Such a succession was studied
in Provence and 7 stages of development were defined using criteria of struc-
ture of the vegetation. The bird communities of each of these stages were cen-
sussed by the I.P.A. method (Blondel et al., 1981). Table 3 gives the list of
species found in each  habitat and figure 1 the proportion of the three main
biogeographical categories along the gradient: birds of steppes and grass-
lands, mediterranean species, boreal sylvatic birds (categories compiled from
Voous, 1960; Moreau, 1966; Blondel, 1981). The main result of this analysis
is that nearly all the species of stage 1 belong to faunal types originating
either from the steppes of the southern Palearctic (Turkestanian-Mediterranean
and Palaeoxeric faunal types of Voous 1960, i.e. Otis tetrax, Burhinus oedi-
cnemus) or from Palaearctic grasslands (Alauda arvensis) whereas all the spe-
cies of stage 7 (forest) are non mediterranean palaearctic forest species.

In the mediterranean-like shrublands, especially in stages 3, 4 and 5, we
find three sets of species: 1) some species of steppes and grasslands which
manage to colonize the patches of very low scrub or nearly bare ground between
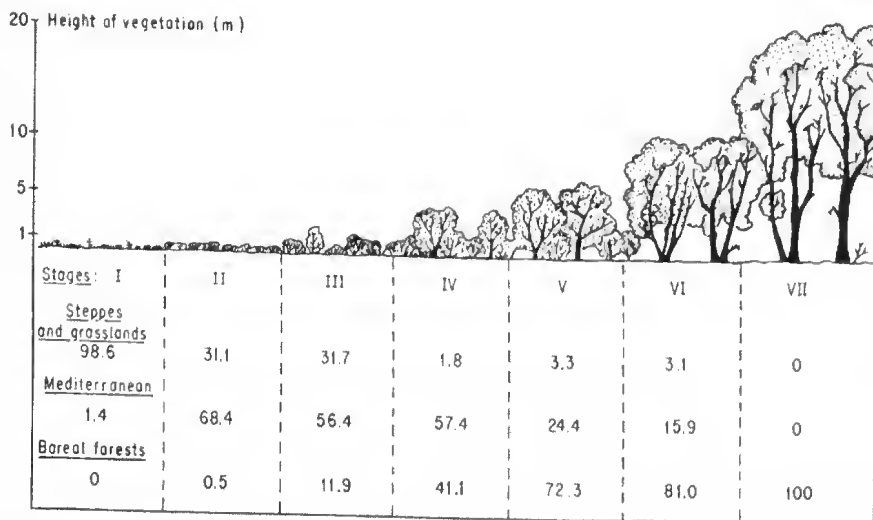the bushes (Anthus campestris, Oenanthe hispanica, Lullula arborea, Alectoris

F i g. 1. Biogeographical composition of the bird communities in seven stages of a succession of Holm oak Quercus ilex in Provence. The trend is characterized by a regular decrease of mediterranean species and species of open habitats (steppes and grasslands) and an increase of medioeuropean species in the old climactic-forest. See text for further explanations (calculated from Blondel, 1981, Appendix 2: 382)

rufa), 2) some ecologically tolerant non mediterranean forest species which spread out from the sylvatic habitats into the highest matorrals (Aegithalos caudatus, Phylloscopus collybita, Garrulus glandarius, Turdus merula, Sylvia atricapilla, Accipiter nisus, Parus major, Erithacus rubecula) and 3) a few truly mediterranean species which evolved within the limits of the Mediterranean biome in an evergreen shrublike vegetation. The best example of this category is the genus Sylvia with five sympatric species, Sylvia conspicillata, S.undata, S.melanocephala, S.cantillans and S.hortensis.

The main conclusion is that out of the 48 species of the gradient, only 8(17%) are of truly mediterranean origin and the only species which can be considered as specifically adapted to and which have evolved in the evergreen mediterranean matorrals are the five warblers just mentioned .

Since these degradated habitats are mostly secondary anthropic formations which are too recent for the achievement of speciation processes, it is not surprising that the bird communities are very poor: in a low garrigue only 4 meters high dominated by Quercus ilex and Quercus coccifera, there are only 12 species totalizing 22.6 breeding pairs/10 ha with Sylvia undata, S.melanocephala, S.cantillans and Luscinia megarhynchos as dominant species whereas in the same type of habitat in Burgundy (Quercus pedunculata) there are 28 species totalizing 44.4 breeding pairs/10 ha (Ferry, Fruchot, 1970: 190-191). The most striking difference between Provence and Burgundy is that the former habitat is too much hot and dry for the penetration of forest species while in the latter, the sylvatic surroundings make them comfortable

598

T a b l e  3. List of species censussed in each habitat of the ecological succession (see legend of fig. 1) SG = birds of steppes and grasslands, M = mediterranean species, BF = birds belonging to european, Palaearctic and holarctic non mediterranean faunal types. The sequence of species is that of their rank of apparition in the gradient from the first habitat to the last (see Blondel 1981 for further details)

| Species | Faunal categorie | Found in habitats |
|---|---|---|
| Circus pygargus | SG | 1 |
| Otis tetrax | SG | 1 |
| Pterocles alchata | SG | 1 |
| Burhinus oedicnemus | SG | 1 |
| Calandrella cinerea | SG | 1 |
| Alauda arvensis | SG | 1 |
| Sylvia conspicillata | M | 2 |
| Anthus campestris | SG | 1-2-3 |
| Oenanthe hispanica | M | 1-2-3 |
| Emberiza hortulana | SG | 2-3 |
| Lullula arborea | SG | 2-3 |
| Lanius excubitor | SG | 2-3-4 |
| Sylvia undata | M | 2-3-4-6 |
| Alectoris rufa | M | 1-2-3-4-5-6 |
| Carduelis cannabina | SG | 2-3-4-6 |
| Pica pica | BF | 2-3-4-6 |
| Clamator glandarius (Afro-tropical) | | 4 |
| Sylvia melanocephala | M | 3-4-5-6 |
| Sylvia cantillans | M | 3-4-5-6 |
| Aegithalos caudatus | BF | 5 |
| Phylloscopus collybita | BF | 5 |
| Luscinia megarhynchos | BF | 3-4-5-6-7 |
| Streptopelia turtur | SG | 4-5-6 |
| Garrulus glandarius | BF | 3-4-5-6-7 |
| Turdus merula | BF | 3-4-5-6-7 |
| Sylvia hortensis | M | 5-6 |
| Sylvia atricapilla | BF | 5-6-7 |
| Circaetus gallicus (Indo-african) | | 6 |
| Accipiter nisus | BF | 5-6-7 |
| Hippolais polyglotta | M | 6 |
| Cuculus canorus | BF | 5-6-7 |
| Parus major | BF | 5-6-7 |
| Phylloscopus bonelli | BF | 5-6-7 |
| Erithacus rubecula | BF | 5-6-7 |
| Regulus ignicapillus | BF | 6-7 |
| Picus viridis | BF | 6-7 |
| Fringilla coelebs | BF | 6-7 |
| Sitta europaea | BF | 6-7 |
| Certhia brachydactyla | BF | 6-7 |
| Columba palumbus | BF | 7 |
| Picoides major | BF | 7 |
| Picoides minor | BF | 7 |
| Oriolus oriolus | BF | 7 |
| Parus caeruleus | BF | 7 |
| Parus ater | BF | 7 |
| Parus cristatus | BF | 7 |
| Troglodytes troglodytes | BF | 7 |
| Turdus viscivorus | BF | 7 |

in the first stages of the succession. Thus the difference in the structure of communities between the first stages of ecological successions and the climactic stage are much stronger in Provence than in Burgundy. As an example the mean value of beta-diversity $H'_{\beta}$ between stages 3,4,5 and stage 7 is .81 in Provence instead of .48 in Burgundy (calculated from Blondel, 1979; Ferry, Frochot, 1970). The deforestation and the dramatic degradation of most lowland and semimontane habitats in the Mediterranean under the pressure of man gave rise to a spatial extension of both steppic and mediterranean species which were formerly much less numerous and had a more patchy distribution. On the other hand, there was an important withdrawal of boreal and temperate forest birds and probably a loss of some large species because of the crumbling of favourable habitats into small isolated woodlots.

## THE CHANGES OF MEDITERRANEAN BIRD COMMUNITIES SINCE THE BEGINNING OF THE CENTURY

In the previous sections, only indirect evidence from biogeography and vegetation dynamics could tell us something about the modification of bird communities under the pressure of man. But historical data, some of them very recent, enlighten and confirm the preceding views, at least in southern France where I live.

Rural France is characterized by a general country desertion which started at the end of the XIXth century and was accelerated after the first world war, then the second. Actually, because of an increase in human demography and a very severe exploitation of the vegetation during the second world war, human pressure on natural habitats was very severe between the years 1940 and 1950 and this probably recalled that which prevailed during several millenaries, since the Neolithic or Bronze age (Pons in litt.). But this pression which lasted only one decade or so stopped almost at once just after the war because of the generalization of fossil fuel instead of firewood for machines and domestic use. As a result there is a generalized resumption of vegetation with more and more old coppices which become taller and taller. This results in an important increase of the woody biomass. Simultaneously, botanists notice that this "biological coming back" (= "remontée biologique") is accompanied by a strong subduing of the mediterranean character of the vegetation: "des surfaces occupées par des taillis plus ou moins bas de Chêne vert ont fait place à un taillis haut de Chênes pubescents, des buxaies claires se sont peuplées de Chênes, voire de Hêtres, des lavandaies se sont parsemées de Chênes caducifoliés ayant repris de souches anciennes" (Pons in litt.). An example of this extension of three tree species, Holm oak <u>Quercus ilex</u>, Pubescent oak <u>Quercus pubescens</u> and Alep pine <u>Pinus halepensis</u> is given on Table 4. Incidentally, this evolution of the vegetation raises some questions about the climax in Mediterranean lowlands. It is probable that deciduous oaks, namely <u>Quercus pubescens</u>, should be more widespread than what was formerly believed. This fits well with the fact that the biogeographic origin of the birds of mediterranean forests is the same as that of the birds of central Europe.

When they analyzed the avifaunal changes of the Camargue and its surroundings during one century, Blondel, Isemann (1981) found that out of 30 chan-

T a b l e  4. Evolution of areas (thousands of ha) covered by Quercus pubescens, Quercus ilex and Pinus halepensis in the french mediterranean region since the beginning of the century (after Acherar 1981)

| Species | surfaces in 1904–1908 | surfaces in 1971–1978 | percent change |
|---------|----------------------|----------------------|----------------|
| *Quercus pubescens* | 235 | 306 | + 30.2 |
| *Quercus ilex* | 310 | 227 | − 26.8 |
| *Pinus halepensis* | 114 | 187 | + 64.0 |
| TOTAL | 659 | 720 | +  9.3 |

ges, 6 were extinctions and 24 were new acquisitions (Table 5). Now, if we except water birds with which we are not directly concerned here, many of the new species are medioeuropean forest birds which progressively come back in their former habitats, especially in the Rhône forest,since man stopped cutting wood.

Furthermore in many cases, the dramatic destruction of forests by wood cutting, fire and overgrazing, produced such catastrophic erosion of soils that importent reafforestation programs started in southern France as soon as the end of the last century and are still in progress. As a result, many mediterranean mountains which were almost bare of woody vegetation a century ago are now covered with true forests. The extension of surfaces planted with Alep pine (Table 4) is partly due to human intervention. Although artificial, many of these forests are now inhabited by sylvatic medioeuropean species which drove back species of open landscapes which have invaded such degradated habitats. Thus these forest species were indirectly reintroduced by man (Blondel, 1976).

T a b l e  5. Avifaunal changes of the Camargue since 1840 (Blondel, Isenmann, 1981)

Extinctions : 6

| | | |
|---|---|---|
| *Numenius arquata* | *Lanius collurio* | *Saxicola rubetra* |
| *Melanocorypha calandra* | *Sylvia borin* | *Turdus viscivorus* |

Acquisitions : 24

between 1840 and 1938 : 9

| | | |
|---|---|---|
| *Anas strepera* | *Clamator glandarius* | *Aegithalos caudatus* |
| *Netta rufina* | *Picoides major* | *Garrulus glandarius* |
| *Thalasseus sandvicensis* | *Picoides minor* | *Sylvia atricapilla* |

since 1938 : 15

| | | |
|---|---|---|
| *Ardea cinerea* | *Larus melanocephalus* | *Erithacus rubecula* |
| *Ardeola ibis* | *Columba palumbus* | *Sturnus vulgaris* |
| *Accipiter nisus* | *Streptopelia decaocto* | *Corvus monedula* |
| *Milvus migrans* | *Phoenicurus phoenicurus* | *Troglodytes troglodytes* |
| *Phasianus colchicus* | *Phoenicurus ochruros* | *Phylloscopus collybita* |
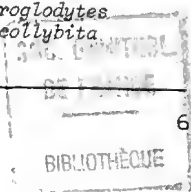
As a matter of fact, the speed of the vegetation improvement is high enough to be noticed by the biologist: this is true not only for botanists but also for ornithologists: during the last 20 years, at least six species (Buteo buteo, Pernis apivorus, Dryocopus martius, Turdus philomelos, Sitta europaea, Parus palustris) which were unknown as breeding birds in Provence have enlarged their distributional area towards the south.

Although somewhat circumstantial, difficult to quantify and rather localized in some parts of the mediterranean region, such examples are good indices of a slow but significant return of mediterranean biotas towards the natural spontaneous equilibrium. There is very little chance that such an equilibrium be fully realized specially since the energy crisis will make more and more demand upon the living biomass so that we are probably at the present time "at the top of the wave". Anyhow, this trend confirms the informations given by palaeobotany, paleontology, biogeography and ecology, namely that plants as well as birds and other animals tend to reoccupy their former habitats thanks to a subduing of human pressure on mediterranean landscapes.

## URBANIZATION

Urban settlements have existed for at least 3500 years, specially in the eastern Mediterranean where there were flourishing pregreek civilisations in the Middle East, Turkey, Crete, etc. The building materials of these ancient cities as well as their spatial organization and the way of life of their inhabitants were probably very favourable for a progressive adaptation of many species to live in the immediate vicinity of man, more or less as commensals. This must be true for such species as Ibises, Storks, Kites, Vultures, Falcons (F.tinnunculus, F.naumanni), Doves, some Owls (Tyto alba, Athena noctua, Otus scops), Swifts, Swallows, Phoenicurus ochruros, Emberiza striolata, Sparrows, several Finches, Sturnus unicolor, Crows etc. To be a successful commensal of human cities it is required to be inquisitive, familiar, gregarious, sociable, cunning, omnivorous but never harmful to human interests. Some large species are very useful as municipal scavengers and were protected for this reason.

Columba livia was the only species to be domesticated and largely spread by man (especially the Romans) but some others were introduced outside their natural range as game birds (Partridges, Pheasants). For most of the species, this commensalism was a starting point for demographic and spatial expansion (direct transportation by man, intentional or not, and spontaneous expansion through cities). Unfortunately very little is known about the role of ancient mediterranean urbanization on the life histories and the range modifications of the species. But close commensal relationship with man, such as that which was described by Meininger et al. (1980) for Corvus splendens whose no populations is known to live away from man must have had important repercussions on the distribution and adaptive characters of the species.

The modernization of cities, specially the biggest ones and human crowds have driven away many of these species, specially big raptors, some of them being on the verge of extinction in some parts of the Mediterranean. This led to a standardization of bird communities in such a way that there are

very few differences between them whatever their geographical location in Europe. Marchetti, Gallner (1976) have analyzed the dynamics of bird communities along a gradient of increasing urbanization from the periphery to the center of the city of Marseille. Their data allowed me to compare the distributional range of the birds of the city with their biogeographic characters. In a previous paper, Blondel, Huc (1978) defined an index of geographical distribution for each of the 264 species of birds breeding in France. This was done from the Atlas des oiseaux nicheurs de France (Yeatman, 1976). If we calculate the average value of his index for all the species in each stage of our gradient of urbanization we see that the higher the degree of urbanization, the more widespread in France are the bird species (Fig. 2). Actually, most of the birds which have a southern distribution in Europe (underlined on table 6) are in the upper part of table 6, that is to say in habitats where there is still some mediterranean vegetation. In the two last stages of most severe urbanization (stages 6 and 7), all the species except Sylvia melanocephala can be found in any other european city.

From this it can be concluded that unfortunately modern mediterranean large cities cannot tell us anything about the history of synanthropisation and its role on the patterns of distribution and adaptive characters of the species involved. Actually we could discuss at length the patterns of distribution and community organization of the birds within the city but this would be out of the scope of this paper and our conclusions would be about the same as those of many other papers on this subject elsewhere in Europe (see for instance Nuoverta,1971; Davis, Glick, 1978). It has been suggested (Erz, 1966) that many of the species commonly found in the european large cities belong to a pool of more or less man-adapted populations which exchange propagules between themselves in the archipelago of cities and which are more or less isolated from populations of the peripheric natural habitats. Such an hypothesis could hold true for some species but not for others; in any case, it remains highly speculative and has to be tested by demographic and genetic studies.

CONCLUSION

The overall conclusion which merges from the set of data which have been collected can be summarized as follows: Because of the privileged geographical situation of the Mediterranean basin at the limit between the great continental Eurasian and African land masses and in close proximity to the semi-arid habitats to the south and to the temperate biome to the north, the richness of the bird fauna is exceptionally high (335 breeding species on an area of ca 2 970 000 $km^2$). This richness was enhanced by the great physiographical and geobotanical diversity of the region. Hence the juxtaposition of faunas of very different origin since we can find species of boreal fir beech forests and birds of xeric steppes only a few kilometers apart but at different elevations. Contrary to what was formerly believed, this situation exists since the beginning of the Pleistocene but the extent of the different types of habitats has changed greatly according to the prevailing climates. But even at the climax of the last glaciation which was the most severe, the thermophilous species could survive locally thanks to the diversity of topographi-
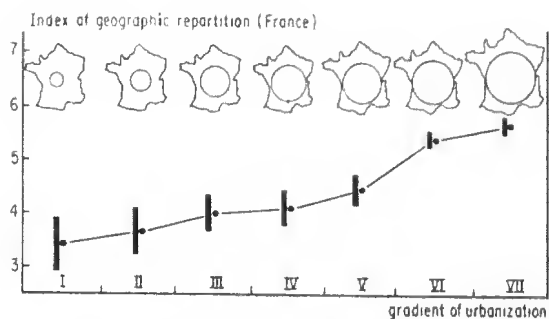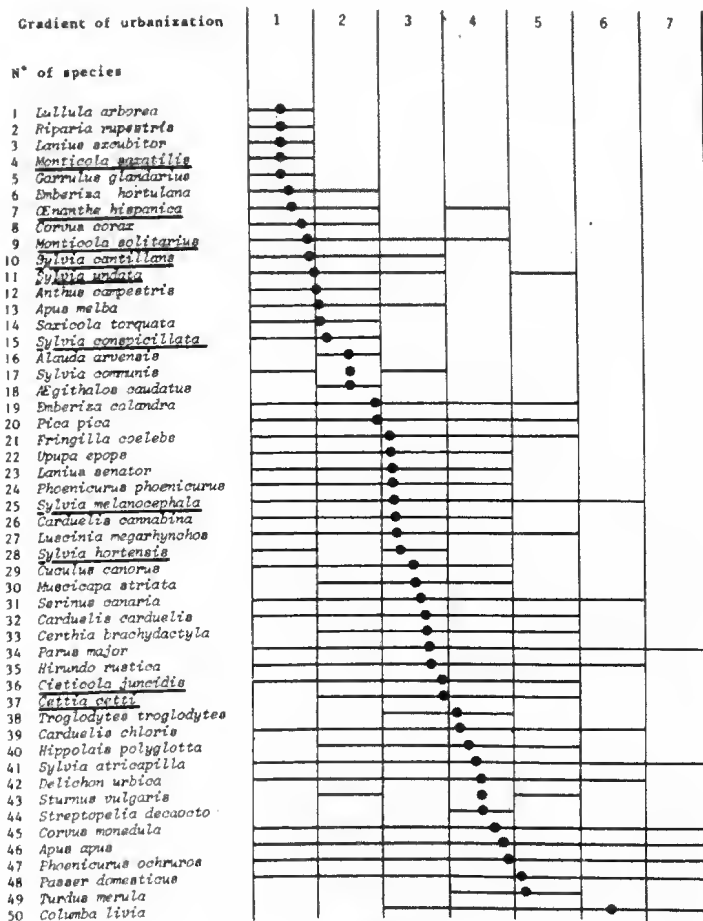
F i g. 2. Indices of geographic repartition in France of the bird communities of seven stages of increasing urbanization in the city of Marseille. While most of the species of first stage (open scrub habitat at the periphery of the city) are mediterranean species localized in southern France (low index of repartition, small symbol circle inside the sketch of France), all the species of stage 7 are widely distributed in France (calculated and drawn from Marchetti, Gallner, 1976; Blondel, Huc, 1978).

cal situations as it is strongly suggested by the persistance of a truly mediterranean vegetation. During the Atlantic optimum (7500 - 4500 BP), most of the lowlands and mountains up to the tree limit were mainly forested with both deciduous trees and conifers. On the other hand, mediterranean habitats such as matorrals were localized and patchily distributed according to local situations, natural catastrophes such as fires, etc. Pollenanalyses have shown that as early as the Neolithic, some 5000 years ago, the first traces of human action on the environment became apparent with discontinuities in the pollinic diagrams and apparition of domesticated cereals. From this epoch onwards, human pressure never stopped and among the main consequences of this action, there was an increase of formations dominated by the Holm oak Quercus ilex at the expense of the broad leaf oaks and a tremendous spatial generalization of matorrals and garrigues. Moreover, modifications effected by man in the sense of habitat simplification (grazing, felling, fires) in land management (creation of new habitats) and in subdivision of the landscape enhanced the mosaic character of the environment. As a consequence, the history of bird faunas is characterized by a strong decrease of forest species which are the same as those of Central Europe to the advantage of more thermophilous species: mediterranean and steppic. The anthropic character of most matorrals probably explains why there are so few species in this kind of habitat.There were probably too small in extension and too patchy for speciation processes to take place. For this reason and contrary to plants and insects, there are very few truly mediterranean species and the bird fauna of the Mediterranean is a mixture of species of very different biogeographic origin. The softening of human pressure for one century finds expression in the return of sylvatic medio-european communities. In other words, the history of bird faunas in the Mediterranean is characterized by a periodic shifting of biotas according to the vicissitudes of the climate and to the action of man.

Many points remain obscure and deserve further studies, for instance the

T a b l e  6. Ordination of the 50 species of birds breeding in the city of Marseille according to the position of the center of gravity (barycentre = black dots) of their distribution along a gradient of 7 stages of increasing urbanization. The horizontal lines represent the number of stages in which each species occurs. Species of mediterranean biogeographic origin are underlined. See text for explanations (calculated after Marchetti, Gallner, 1976)

| Gradient of urbanization | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|---|---|---|---|---|---|---|---|

N° of species

| N° | Species |
|---|---|
| 1 | *Lullula arborea* |
| 2 | *Riparia rupestris* |
| 3 | *Lanius excubitor* |
| 4 | *Monticola saxatilis* |
| 5 | *Garrulus glandarius* |
| 6 | *Emberiza hortulana* |
| 7 | *Œnanthe hispanica* |
| 8 | *Corvus corax* |
| 9 | *Monticola solitarius* |
| 10 | *Sylvia cantillans* |
| 11 | *Sylvia undata* |
| 12 | *Anthus campestris* |
| 13 | *Apus melba* |
| 14 | *Saxicola torquata* |
| 15 | *Sylvia conspicillata* |
| 16 | *Alauda arvensis* |
| 17 | *Sylvia communis* |
| 18 | *Ægithalos caudatus* |
| 19 | *Emberiza calandra* |
| 20 | *Pica pica* |
| 21 | *Fringilla coelebs* |
| 22 | *Upupa epops* |
| 23 | *Lanius senator* |
| 24 | *Phoenicurus phoenicurus* |
| 25 | *Sylvia melanocephala* |
| 26 | *Carduelis cannabina* |
| 27 | *Luscinia megarhynchos* |
| 28 | *Sylvia hortensis* |
| 29 | *Cuculus canorus* |
| 30 | *Muscicapa striata* |
| 31 | *Serinus canaria* |
| 32 | *Carduelis carduelis* |
| 33 | *Certhia brachydactyla* |
| 34 | *Parus major* |
| 35 | *Hirundo rustica* |
| 36 | *Cisticola juncidis* |
| 37 | *Cettia cetti* |
| 38 | *Troglodytes troglodytes* |
| 39 | *Carduelis chloris* |
| 40 | *Hippolais polyglotta* |
| 41 | *Sylvia atricapilla* |
| 42 | *Delichon urbica* |
| 43 | *Sturnus vulgaris* |
| 44 | *Streptopelia decaocto* |
| 45 | *Corvus monedula* |
| 46 | *Apus apus* |
| 47 | *Phoenicurus ochruros* |
| 48 | *Passer domesticus* |
| 49 | *Turdus merula* |
| 50 | *Columba livia* |

consequences of human impact on the patterns of distribution of species within and outside the mediterranean basin and the effect or urbanization on adaptive characters of the species.

SUMMARY

Palaeobotany, paleontology as well as biogeographical and ecological cues support the hypothesis that at the end of postglacial times, during the climatic optimum (Atlantic period, 7500 - 4500 BP), the bird faunas of the mediterranean area were dominated by medioeuropean forest species in the deciduous lowland and conifer montane forests which were widespread everywhere in the mediterranean basin. The truly mediterranean component of the bird communities was never important but always present even at the maximum of glacial times because of the permanent existence of patches of mediterranean matorrals in which some species evolved (i.e. genus Sylvia). The consequences of human pressure which is very strong since at least 4000 years are a dramatic reduction of forests and an extension of matorrals which are only secondary formations. This found expression by a shrinking back to the north of forest species and a progression of the few mediterranean species and of the thermophilous southern species originating from steppic and semi-arid regions. As an example it is shown that the few relictual patches of old climatic forests support bird communities which are very similar to those of central Europe with no mediterranean species. Thanks to the industrial revolution in the XIX° century and the two world wars, there is since one century a general country desertion by man. As a consequence there is a significant return of forest vegetation with its accompanying birds. This trend confirm the informations given by palaeobotany, paleontology, biogeography and ecology, namely that biotas tend to reoccupy their former habitats thanks to a subduing of human pressure. So, the history of bird faunas in the Mediterranean is a geographic balance between "northern" medioeuropean avifaunas and "southern" avifaunas originating mainly from the steppic and semi-arid regions to the east and to the south of the Mediterranean. At a long term this balance is produced by climatic vicissitudes and/or by human impact on the landscapes. Finally the role of urbanization on the distribution patterns of some species is discussed.

R e f e r e n c e s

Acherar M. La colonisation des friches par le Pin d'Alep (Pinus halepensis Mill.) dans les basses garrigues du Montpelliérais. Thèse, Montpellier, 1981.

Beug H.J. - Rev. Palaeobot. Palynol., 1967, 2, p. 271-279.

Blondel J. - Ann. Sci. Forest., 1976, 33, p. 221-245.

Blondel J. Biogéographie et Ecologie. P.: Masson, 1979.

Blondel J. - In: Mediterranean-Type shrublands. Coll. Ecosystems of the World, vol. 11 / Eds. F. di Castri, D.W.Goodall, R.L.Specht. Amsterdam: Elesevier, 1981, p. 361-385.

Blondel J. Ecologia Mediterranea, 1982.

Blondel J. Proc. XVIII Int. Orn. Cong.,1986.

Blondel J., Ferry C., Frochot B. - In: Estimating the numbers of terrestrial birds. Stud. Avian Biol. 6 / Eds. C.J.Ralph, J.M.Scott. Cooper Orn. Soc., 1981, p. 414-420.

Blondel J., Huc R. - Alauda, 1978, 46, p. 107-129.

Blondel J., Isenmann P. - Guide des Oiseaux de Camargue. Neuchatel. Delachaux and Niestlé, 1981.

Davis A.M., Glick Th.F. - Environm. Conserv., 1978, 5, p. 299-304.

Erz W. - Ostrich suppl., 1966, 6, p. 357-363.

Ferry C., Frochot B. - La Terre et la Vie, 1970, 24, p. 153-250.

Marchetti M., Gallner J.Cl. Recherches sur l'écologie des oiseaux nicheurs de la zone urbaine de Marseille. Marseille: Thèse, 1976.

Meininger P.L., Mullié W.C., Bruun B. - Le Gerfaut, 1980, 70, p. 245-250.

Moreau R.E. - Ibis,1954, 96, p. 411-431.

Moreau R.E. The Bird faunas of Africa and its islands. Acad. Press, 1966.

Mourer-Chauviré C. Les oiseaux du Pléistocène moyen et supérieur de France. Lyon: Thèse, 1975.

Nuorteva P. - Ann. Zool., ˜enn., 1971, 8, p. 547-553.

Pons A. - In: See Blondel / Eds. F. di Castri, .W.Goodall, R.L.Specht, 1981, p. 131-138.

Pons A., Quézel P. La mise en place, l'évolution et la caractétisation de la flore et de la végétation méditerranéennes. Naturalia Monspeliensia, 1981. 231 p.

Spitz F., Le Louarn H. -In: Problèmes d'Ecologie: Ecosystèmes terrestres / Eds. M.Lamotte, F.Bourlière. P.: Masson, 1978, p.102-110.

Suc J.P. - Bull. Ass. Fr. Et. Quat., 1973, 34, p. 13-24.

Triat-Laval H. Contribution pollenanalytique à l'histoire tardi- et postglaciaire de la végétation de la basse vallée du Rhône. Marseille: Thèse, 1978.

Vernet J.L. - Et. Quat. Mém., 1972, 1, p. 329-339,341-343.

Voous K.H. Atlas of European Birds. Amsterdam. Nelson, 1960.

Yeatman L. Atlas des oiseaux nicheurs de France. Soc. Orn. Fr. Paris, 1979.

# URBANIZATION AS A TEST OF ADAPTIVE POTENTIALS IN BIRDS

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This presentation is a condensed version of a fuller review to be published separately. Thersfore ths literature quotations ara hers restricted to a minimum. My aim is a present-day synthesis of the knowledge on bird colonizations of urban habitats, restricted to the European conditions. The generalizations offered in this papsr have a tentative character bsing formulated intuitively though on the basis of largs material from almost a hundred of towns and cities. Such an approach was unavoidable because of a limited statistical comparability of existing quantitative urban studies (Tomialojc, in prep.). There are also frequent pitfalls in the urban-non-urban comparisons, as not every piece of nominally "urban" land offers real urban ecological conditions, and, equally, not every non-urban area represents a natural state. For fruitful urban-nonurban comparisons clear (typical or most advanced) conditions should be selectsd, e.g. the natural state of arboreal birds should be looked for in extensive forests resistent to the influences from the neighbouring farmland. Several studies have evsn failed to disclose the sharp differences which exist in nature, because they have concentrated on only a small section of a continuous habitat gradient. The conclusioncan be equally confusing when someone pulls together the data picked up randomly from the whole gradient of man-made and man-transformed habitats and, while analysing them, divides the material only into two categories: urban and non-urban or forest versus non-forest. The only promising procedure is to split data into at least three categories; between sxtremal categories the differences may appear to be significant.

The comparison of extreme states, primaeval and urban, under which a spscies can thrive is of special scientific value (Tomialojc, 1980, 1982).Urban studies can offer the "experimental" conditions; this opportunity was too rarely sxploitsd for the studies in population dynamics.

## The reasons for bird colonizations of urban areas·

Three groups of factors can be rscognized here: the attracting forces (active colonizations), the inhibiting factors and the pressures from outside (passive colonizations).

The importance of the former two groups of factors has already been wsll documentea in literature. The disagresment occurs in the case of forced (passive) colonization. The question is: does the colonization of urban areas depend on the abundance of birds in the surrounding natural habitats? W.Erz (1966) offered a negative answer to it. Nowadays, however, the importance of "superabundant" individuals from optimal habitats for the subsequent colonization of suboptimal ones has become well recognized (Klujver, 1951; Brown, 1969; Krebs, 1971; Watson, Moss, 1970, etc.). It remains to be checked how frequently this surplus occurs as a natural phenomenon or when

it results from earlier anthropogenic disturbances (Brown, 1969). The following arguments speak in favour of forced urban colonizations: a) The pronounced parallelism in the patterns of geographic distribution of breeding densities in urban and non-urban populations of a species, which is observed on the continental and on the local scale (Bozhko, 1968; Saemann, 1969; Tomialojc, Profus, 1977). The successful colonizations usually start from the most dense, eurytopic and expansive wild populations of a species. b) Before a successful colonization several unsuccessful attempts were observed, which suggests that the frequency of intrusions is of crucial importance here (Tomialojc, 1976). c) High density of non-urban or "source" populations can be either primaeval and wide-spread over several habitats (as it is in the quantitative centre of a species breeding range), or primaeval and local (as it is on the margins of the breeding range, when e.g. arboreal birds penetrate open landscape, the grassland, semidesert or tundra), or finally secondary and (usually) local. The last case results from man-induced reduction of forests and formation of the island-like woods. In all these three situations there exists either primaeval or secondary superabundance of individuals (at least males) expelled from the "source" populations by their social mechanisms. Thus, at an initial period of colonization the human settlements frequently represent a suboptimal habitat with the colonizers presumably carrying the inferior competitive qualities. d) A west-east gradient of decreasing total bird density can be observed over the Europe, not only the south-north directed one (Novikov, 1960; Tomialojc, Walankiewicz, Wesolowski in prep.). It is still not known to what degree it results from the natural climatic cline (oceanic-continental) and to what degree from differences in the intensity and duration of human transforming activity. The reduction of the once forest dominated cover of the Western Europe presumably yielded the increase in the local (within remaining patches of woods) bird density of several forest species because of: a decreased predation pressure (Tomialojc, 1980 and in prep.), lowered pressure of man himself, the natural and man-induced amelioration of the climatic, chiefly wintering (Kalela, 1950), conditions, and the secondary sedentariness of the once migratory West-European forest birds (Lack, 1947, 1966). All this allows to expect the development of "superabundance" in some western non-urban bird populations, which in turn could force the colonization of human settlements.

The additional circumstance is that the success in invading the urban areas is more probable in a region where "source" populations have undergone first-step changes "cultural and/or inherited), which frequently were incorrectly classified as the primaevally possessed "preadaptations" to man-made habitats. Our recent studies in the close-to-primaeval forest of Bialowieza clarify this interpretation (Tomialojc, Walankiewicz, Wesolowski, in prep.). The absence of deep preconditional transformations seems to be responsible for the conservatism of several East- or North-European bird populations, as well as those from some afforested regions of Western and Central Europe, or finally, as those native birds on other continents which fail to compete with the Europe-originated invadors.

## The "monophyletic" of "polyphyletic" origin of urban populations

Impressive expansion of some urban populations in Europe, chiefly of Tur-

dus merula, laid basis for another controversy. It was believed that such populations develop in a single town or region (Steinbacher, 1942; Heyder, 1955; Graczyk, 1959, 1963; Koskimies, 1956; Ljunggren, 1969, etc.). Closer examination yields an alternative, compromising, explanation:

a) There is no firm reason to assume "monophyletic" origin of urban populations to be a rule. The idea that there was no exchange of individuals between urban and non-urban Blackbirds or Woodpigeons has been rejected (Erz, 1966; Mulsow, 1976; Tomialojc, 1980). The eastward expansions may be even the result of a geographically expanding complex of factors itself.

b) Some town-to-town movements certainly occur, at least on a local scale. They become actual expansions when an urban population continues to spread outside the species breeding range.

c) Even a few immigrants from a distant city may stimulate local wild birds, by launching the imitation, to invade urban areas. Thus, only first stimulus would be transferred from town to town as a new "tradition", and a very limited actual genetical descendency can be introduced in this way. Presumably the success of colonizing individuals depends on the readiness of the non-urban populations to follow their example and to support genetically the development of a local urban population.

There are several arguments for the "polyphyletic" origin of some urban populations: 1) Several distant centres of obviously independent species colonizations are known. For example in Columba palumbus these were: NW-Europe, Milano, Madrid, Bagdad (Tomialojc, 1976); in T.merula these were: NW-Europe and presumably Wroclaw which contained some urban Blackbirds as early as 1857, according to Pax 1925 ; b) The eastward expansion of urban T.merula was speeded up by known or suspected, intentional or accidental, introductions of these birds by humans (Fig. 1); c) Even in very remote places such as the Bialowieza village, which is situated amidst vast forests in Eastern Poland, the synanthropic very fame populations of Turdus philomelos, T.merula, T.iliacus, Erithacus rubecula, Carpodacus erythrinus and Garrulus glandarius have developed independently of their West- or North-European conspecifics.

## The degree of isolation between urban and non-urban bird populations

This problem urgently needs special field studies. At present it can be only speculated that the degree of genetic isolation varies depending on the species, its migratory or resident status, and on the size and structure of urbanized areas. There could be three possibilities: a) Absence of isolation-Here both groups of birds interbreed freely and constitute a common local population. Such situation is most likely in certain relatively form small birds easily penetrating human settlements, as well as in the migratory or nomadic species in which a significant shuffling of individuals occurs during the nonbreeding period. Examples include: Parus major and P.caeruleus in Central European towns, Hippolais icterina or Muscicapa striata. b) Moderate isolation - Here two more or less distinct local populations co-occur and differ in their response to man . However, even in classical cases of T.merula and C.palumbus some degree of interchange between urban and non-urban populations occurs (Erz, 1966; Mulsow, 1976; Tomialojc, 1980). In vast cities the
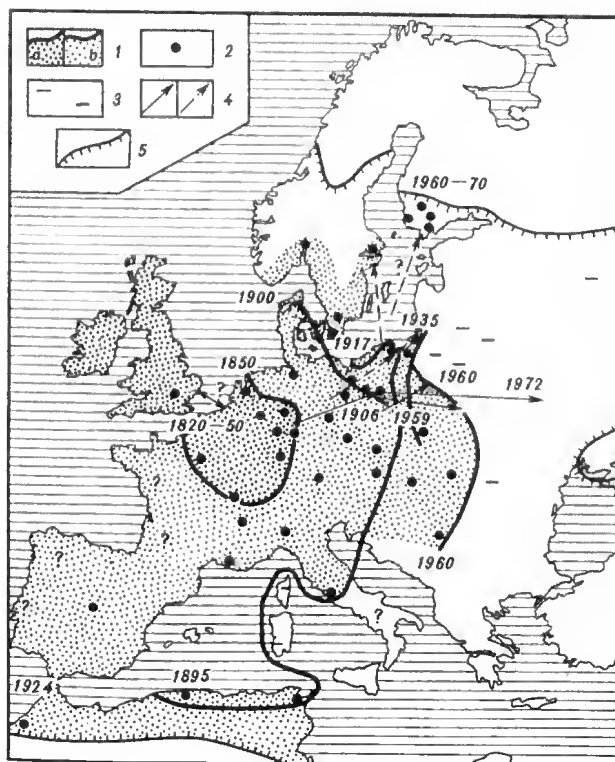
F i g. 1. The expansion and the present distribution of urban Blackbirds
(Turdus merula)

1 - areas occupied by the year X; 2 - main towns with urban Blackbirds;
3 - main towns without urban Blackbirds; 4 - known or suggested (dashed
arrows) introductions of urban Blackbirds by man; 5 - species breeding
range

inbreeding should be stronger than in smaller human settlements, though no
critical data are available. c) Almost total or total isolation - This is the
case when a synanthropic population expands beyond the original species breed-
ing range. The contact with wild population is very limited here or can be
easily broken (Johnston, Klitz, 1977). In the case of a strong northward ex-
pansion some species enter new climatic zones, which can reorganize their ge-
netic pools (Mayr, 1926; Gladkov, 1958). Again, however, there are no de-
tailed studies.

Two future opposite tendencies are possible: the expanding urban areas will
tend to increase the spatial isolation from wild populations. However, the in-
creasing presence of green spaces in towns and the recent colonization of
them by predators will lead to the convergent evolution of urban and rural
populations.

Changes in bird ecology in the course of urbanization. Theoretically, the
most important changes in ecology are those which increase the individual
fitness. In several cases this has been demonstrated for urban birds, e.g.

the urban Woodpigeons produce 4-6 times, sometimes 27 times, more young per season than their wild conspecifics, and suffer 40-70 times lower adult mortality in their urban breeding places (Tomialojc, 1980 and in prep.). Better urban survival has also been documented in other bird species (Snow, 1958; Mulsow, 1976; Monaghan, 1979, etc.). This phenomenon yields several consequences like high breeding density, and several differences in behaviour and ecology. They are mainly the opportunistic deviations from a modal value which dissappear if usual selection is restored.

The primaeval mechanisms of population regulation or limitation seem to be replaced by a secondary set of factors playing the role in urban areas densely populated by birds. Competition for food becomes more frequent while the pressure of natural enemies loses its limiting influence. This possibility has been too rarely investigated again (Vladyshevskij, 1975; Tomialojc, 1980, 1982).

### The nature of bird adjustments to urban life

Knowledge of this aspects remains scanty. The attempts to attract our colleagues ethologists, physiologists and geneticists to detailed studies of this problem emerge as the most urgent task. The following possibilities deserve research:

1) Morpho-physiological and behavioural true adaptations (genetically fixed);

2) Environmentally acquired phaenotypical adjustments, mainly the behavioural ones ("cultural adaptations");

3) Undirected deviations from the modal values resulting from the abatement of the normalizing action of natural selection and from the increased intrapopulational tension (overcrowding).

According to Dobzhansky et al. (1977) any inherited behaviour can be perfectioned by experience, and probably any learned behaviour relies at least partially on a genetical basis. The inherited element was found or was suspected as contributing to the following urban changes: increasing sedentariness (Graczyk, 1963; Berthold, 1975, 1979) and increasing resistence to the winter climate, the tameness of urban individuals (by selection of genetically less nervous individuals or those with inherited better learning abilities), changing levels of territorial aggresiveness, smaller clutch-size, etc. For a long time it was assumed that the adaptive evolutionary changes were a very slow process. Lack (1965) expected that the bird populations thriving in man-transformed environments might not yet have adapted precisely to these new conditions. The latest studies of van Noordwijk, van Balen and Scharloo (1981, 1981a) have questioned this belief and indicated that considerable genetic changes can evolve even within a period of five generations, i.e. within a decade in the case of the comparatively short-lived Parus major. In view of this some hundred, or even thousand year old, urban populations were potentially able to develop significant genetic differences – the true adaptations. For example, both the clutch size and the timing of breeding have turned out to be partly genetically determined in some bird species. A considerable inbreeding of some urban populations can be expected as an analogue to that found in an insular population of Parus major (van Noordwijk,

Scharloo, 1981). It may turn out that pronounced adaptability of western populations and the conservatism of some eastern ones results partly from a different degree of isolation between their urban and non-urban birds. Resident werstern' forms may develop the adaptations to new local conditions quicker than the eastern migratory ones. It might be that the synanthropy relies not so much on cultural adjustments, as it was commonly believed, but in a considerable degree also on genetical adaptations. The mainly behavioural differences of the first period can be supported by the subsequent morpho-physiological adaptations. According to Vladyshevskij (1975) this can be expected at least in the following features:

- different stereotype of foraging movements of some urban birds;
- tendency to longer feeding flights;
- tendency to stay in open habitats, far from shelter (with an parallel abatement of pressures on the camouflaging elements in plumage colouration - L.T.);
- increasing residency with subsequent changes in dispersal and territoriality patterns and in morpho-physiology.

The character of urban areas permanently changes with time, however,which presumably will disrupt the perfectioning of some adaptations and favour in many cases the cultural adjustments.

Only after proper studies, taking into account the genetical and ecological aspects, could we estimate to what extent the adjustments of birds to man-made environment depend on selecting genetical preadaptive traits, so that they rely on the subsequent genetical perfectioning (postadaptation), and to what degree on learning processes.

### SUMMARY

This is a short version of a fuller review to be published separately. It is concluded that the bird colonizations of towns depend on the situation in their wild populations. The expansions of urban populations from town to town partly rely on "cultural" transmissions. The degree of genetical isolation from wild populations presumably vary between species and towns. The nature of bird adjustments to urban life urgently needs studies.

### R e f e r e n c e s

Berthold P. - Avian Biology, 1975, 5, p. 77-128.
Berthold P. - Vogelwarte, 1977, 29 Suppl., p. 4-15.
Bozhko S.I. - Aquila, 1968, 75, p. 141-149.
Brown J.L. - Wilson Bull., 1969, 81, p. 293-329.
Dobzhansky T., Ayala F.J., Stebbins G.L., Valentine J.W. Evolution. San Francisco: Freeman, 1977.
Erz W. - In: Proc. 2nd Pan-African Orn. Congr. 1964. Suppl. to Ostrich, 1966, p. 357-363.

Gladkov N.A. - Ornithologija, 1958, 1, p. 17-34.

Graczyk R. - Ekol. pol A, 1959, 7, p. 57-82.

Graczyk R. - Roczn. WSR Poznań, 1963, 17, p. 21-71.

Graczyk R. - Roczn. WSR Poznań, 1974, 65, p. 49-65.

Heyder R. - Beitr. Vogelkd., 1955, 18, p. 51-60.

Johnston R.F., Klitz W.J. - In: Granivorous birds in ecosystems: the house
    sparrow / Eds. J.Pinowski, S.Ch.Kendeigh. Cambridge, 1977.

Kalela O. - Orn. Fenn., 1950, 27, p. 1-30.

Klujver H.N. - Ardea, 1951, 39, p. 1-135.

Koskimies J. - Orn. Fenn., 1956, 33, p. 77-95.

Krebs J.R. - Ecology, 1971, 52, p. 2-22.

Lack D. The life of Robin. L.: Witherby, 1947.

Lack D. - J. anim. Ecol., 1965, 34, p. 223-231.

Lack D. Population studies of birds. Oxford: Clarendon, 1966.

Ljunggren L. - Viltrevy, 1968, 5, p. 435-504.

Mayr E. - J. Orn., 1926, 74, p. 571-671.

Monaghan P. - Ibis, 1979, 121, p. 475-481.

Mulsow R. - Hamb. avifaun. Beitr., 1976, 14, p. 135-146.

Van Noordwijk A.J., van Balen J.H., Scharloo W. - Netherl. J. Zool., 1981,
    31, p. 342-372.

Van Noordwijk A.J., van Balen J.H., Scharloo W. - Oecologia (B.), 1981a, 49,
    p. 158-166.

Van Noordwijk A.J., Scharloo W. - Evolution, 1981, 35, p. 674-688.

Novikov G.A. - Zool. Zhurn., 1960, 39, p. 433-447.

Pay F. Wirbeltierfauna von Schlesien. B.: Borntraeger, 1925.

Saemann D. - Der Falke, 1968, 16, p. 81-86.

Snow D. - Ardea, 1969, 57, p. 163-171.

Steinbacher C. - J. Orn., 1942, 90, p. 342-360.

Tomialojc L. - Acta zool. Cracov., 1976, 21, p. 585-631.

Tomialojc L. - Pol. ecol. Stud., 1980, 5, p. 141-220.

Tomialojc L. - In: Animals in urban environment / Eds. M.Luniak, B.Pisarski.
    Wroclaw: Ossolineum, 1982, p. 131-139.

Tomialojc L., Profus P. - Acta orn., 1977, 16, p. 117-177.

Vladyshevskij D.V. Ptitsy v antropogennom landshafte. Novosibirsk: Nauka,1975.

Watson A., Moss R. - In: Dynamics of populations / Eds. Den Boer, S.Gradwell.
    Waageningen, 1971, p. 167-218.

BREEDING ECOLOGY OF THE TWO POPULATIONS OF TURDUS GRAYI AT
.LOCALITIES OF DIFFERENT HUMAN INFLUENCE IN PANAMA LOWLAND

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The aims of the present study were: 1) to compare the breeding ecology of
a tropical species with another in the European temperate zone (Dyrcz,
1963, 1969), 2) to make a comparison between populations of Clay-coloured
Robins, studied in two ecologically different localities.

STUDY AREA AND METHODS

I carried out my study from March to June 1979 in the former Panama Canal
Zone, on two sample areas about 15 km apart. The first area (27.3 ha) was
situated in the Summit Gardens, south of Gamboa. It comprised part of an ar-
boretum and nursery with mown grass, large scattered trees, clumps of bushes
and ornamental bamboo. Summit Gardens is surrounded by forest with no settle-
ments in the vicinity. The other area (3.6 ha) was in Morgan's Gardens in the
vicinity of Balboa. This is a private plant nursery, with many high trees,
open grassy patches and clumps of bushes, surrounded by deforested areas with
some settlements.

I searched both study areas several times during the breeding season in
order to find and check all Clay-coloured Robin nests, as soon as possible
after nest-building started. Eighty three active nests were found. The nest-
lings were weighed using a Pesola spring balance, and samples of nestling
food were collected using the neck collar method (e.g., Kluijver, 1933). Four
hundred sixty six samples containing 1045 items were collected and preserved
in 70% alcohol for further analysis.

RESULTS

Breeding losses and fledgling success. Breeding losses were caused mainly
by predation (Table 1). Predation was lower during the dry season than during
the rainy season which is in accordance with Morton (1971) results. Out of
forty one occupied nests present during dry season, six (5%) were predated
(but most of these close to the beginning of rainy season). Out of sixty
three nests occupied during the rainy season, thirty one (49%) were preda-
ted ($\chi^2$ = 13.0, P < 0.001). Predation rate increased during the course of
the breeding season, being highest at the end of the season. The rate of
predation was not higher during the period of the highest active nest densi-
ty in study areas.

Altogether I spent 21 hours watching Clay-coloured Robin broods. During
this time I saw two attempts, made by Variegated Tree Squirrel Sciurus va-
riegatoides, to rob the nest. I noticed also a rather mild aggressive react-
ion of Robin parents to a male of Long-tailed Grackle (Cassidix mexicanus)
and two Squirrel Cuckoos Piaya cayana foraging close to the nest. There were
many indications that ground animals play important role as Clay-coloured
Robin brood predators. The indications can be listed: 1) the Robin's tendency
to locate the nest on isolated tree, 2) its predilection to build its nest
on flexible branches difficult to climb, than by the trunk (Table 2, 3) the
lower predation on nests situated on the palm-trees which have flexible
leaves and trunks that are hard to climb (Table 3 , 4) the higher losses
among nests situated lower (Table 4).

Table 1. Reason of brood losses

|  | N of broods |
|---|---|
| Predation | 37 |
| Ants | 1 |
| Wind | 1 |
| Eggs unfertilized | 1 |
| Other | 1 |

Table 2. Percentage frequency of different nest-sites

| Species | N of nests | Nest site | | | |
|---|---|---|---|---|---|
|  |  | Near trunk | Other site | Horizontal branch | Other site |
| Turdus grayi | 124 | 15.4 | 84.6 | 56.4 | 43.6 |
| Turdus merula | 296 | 36.2 | 63.8 | 33.8 | 66.2 |
| $x^2$ |  | 17.7 | | 17.1 | |
| Probability |  | $P < 0.005$ | | $P < 0.005$ | |

Table 3. Losses among broods of Clay-coloured Robin situated on palm-tree in comparison to losses on other plants

|  | n | % broods suffering predation | % successful | $x^2$ | Probability |
|---|---|---|---|---|---|
| Palm tree | 20 | 30.0 | 70.0 |  |  |
| Other plant | 65 | 60.0 | 40.0 | 4.39 | $P < 0.05$ |

Table 4. Brood losses and nest height

|  | n | % broods suffering predation | % successful | $x^2$ | Probability |
|---|---|---|---|---|---|
|  |  | Turdus grayi | | | |
| Below 3.5 m | 33 | 66.7 | 33.3 |  |  |
| Above 4 m | 15 | 46.7 | 53.3 | 0.99 | N. S. |
|  |  | Turdus merula | | | |
| Below 1.5 m | 42 | 54.8 | 45.2 |  |  |
| Above 2 m | 51 | 76.5 | 23.5 | 3.96 | $P < 0.05$ |

There is one more point which should be explained. In contrast to the Blackbird, the Clay-coloured Robin nests are often in very exposed places easy to be spotted by sight. I think that I found the reason after watching the birds. When feeding nestlings the parents forage not far from the nest and often in a quite open landscape. So they can keep eye on the exposed nest when foraging to notice early any approach of a predator. It might be important in the light of my former observation, which suggested that the parents have a good chance to force out so-called small predators.

## COMPARISON BETWEEN TWO STUDIED POPULATIONS

Both studied areas can be considered from the ecological point of view as islands of habitat especially suitable for Clay-coloured Robin breeding. But Morgan's Gardens is an island surrounded by deforested area while Summit Gardens is an island surrounded by forest. I think that it makes difference mainly in predation rates. Obviously there should be more predators in Summit Gardens than in Morgan's Gardens. Indeed, the losses from predation were much lower in the latter locality, and a breeding population density much higher (Table 5). The higher population density made feeding conditions worse, which caused more fruit in nestlings' diet (which is supplementary food of lower quality) to be present, a lower average nestlings' weight, more starving among runts (Table 5). But in gross output, the production of nestling per breeding pair was still two times higher in Morgan's Gardens than in Summit Gardens (Table 5). The general conclusion from a comparison between the two studied populations could be stated that the strategy to settle down in a rather overpopulated place with hard foraging conditions but lower predation paid better than settling down in a place with a better food supply but higher predation (although the probable difference in survival rates of fledglings from two studied areas is not known). It suggests also that low predation is an important cause of the very high population density of Clay-coloured Robin in many former Canal Zone settlements. Another reason might be the presence of shortgrass lawns which make good foraging grounds.

Morton (1971) studied a Clay-coloured Robin population in the Summit Gardens. He found that the breeding season started there earlier then during my study. Taking into consideration my both areas, I found similarly that good proportion of breeding pairs bred during the dry season, when foraging conditions were worse. His main idea is that the Robin starts to breed early in the dry season (March) in spite of animal food scarcity, in order to avoid high predation in the rainy season. The benefit of avoiding predation is partly offset by the necessity to feed relatively non-nutritious fruit to nestlings, which cause some starvation. During the rainy season, Robins fed young more nutritious invertebrata. My study suggested that difference between sites were also important.

T a b l e   5. Comparison between two populations of Clay-coloured Robin

| | Morgan's Gardens | Summit Gardens | Statistic significance |
|---|---|---|---|
| Brood losses from predation in % | 21.7 | 59.6 | $\chi^2 = 4.4$, $P < 0.05$ |
| Breeding density pairs/10 ha | 50.0 | 15.8 | |
| Percentage of fruit in nestlings' food | 43.9 | 17.5 | $\chi^2 = 80.9$, $P < 0.001$ |
| Mean weight of 12 day old nestlings g | 45.7 | 55.2 | $t = 6.01$, $P < 0.001$ |
| N of starving nestlings per successful brood | 0.6 | 0.4 | N. S. |
| N of fledgling per breeding pair | 1.8 | 0.9 | |

The nearly one month difference in average dates of beginning of breeding season between study areas may result from the fact that Morgan's Gardens where breeding started earlier are situated close to the branch of the Canal influenced by tides. At low water level the muddy bottom emerges, so that the birds can find muddy soil, necessary for nest construction, even in a dry season. No such possibility existed in Summit Gardens.

## COMPARISON BETWEEN TURDUS GRAYI AND TURDUS MERULA

This comparison shows a few interesting differences between two species which are connected mainly with the antipredator adaptations and feeding conditions during the breeding season. Blackbird tendency to breed lower, closer to the trunk, often in dense bushes, as well as higher losses among high situated nests suggest importance of avian predator for this species. Longer time-span between completion of the nest and laying of the first egg in Clay-coloured Robin (Table 6) can also be considered as an antipredator adaptation. More fruit in nestling diet, longer nestling period (Table 7), more frequent starving among nestlings and smaller clutch-size in Clay-coloured Robin - all seem to be connected with relative food scarcity during the breeding season. The average weight of 12-day old Robin nestling (55.2 g) consisted 75% of the average adult weight and in Blackbird (unpublished data) only 67%. The reason might be that Robin nestlings left the nest physiologically older or that more Robin nestling with low weight were eliminated by starvation before the 12th day of life.

T a b l e  6. Time-span (days) between nest completion and laying of the first egg

| Clay-coloured Robin | Blackbird (Mizera, 1978) |
|---|---|
| 2-10 ($\overline{x}$ = 5.3, n = 18) | 0-4 ($\overline{x}$ = 1.9, n = 19) |
| t = 6.1, P$<$ 0.001 | |

T a b l e  7. Length (days) of nestling period

| Clay-coloured Robin | Blackbird (Glutz, 1964; Mizera, 1978) |
|---|---|
| 13-18 ($\overline{x}$ = 15.1, n = 16) | 12-19 ($\overline{x}$ = 13.9, n = 32) |
| t = 2.7, P$<$ 0.05 | |

R e f e r e n c e s

Dyrcz A. - Acta orn., 1963, 7, p. 337-385.
Dyrcz A. - Ekol. Pol. A, 1969, 17, p. 735-793.
Kluijver H.N. - Dients, 1933, 69, p. 1-145.
Morton E.S. - Science, 1971, 171, p. 920-921.

# THE TEMPORAL AND SPATIAL SCALES OF MIGRATION IN RELATION TO ENVIRONMENTAL CHANGES IN TIME AND SPACE

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## INTRODUCTION

Because habitats change in suitability and resource availability through time, birds that have specific habitat requirements with regard to these measures must change location and seek new habitats elsewhere if they are to survive and reproduce. The spatial movements of birds, whether maintenance, dispersal, or migratory, are evolutionary strategies that express the expectation of temporal change in conditions at the present locality. If the resources in a suitable habitat can support a certain number of individuals during a period of high resource availability and only a fraction of that number during a period of low resource availability, then during the latter period some of the individuals in the population must move and seek other suitable habitats or perish. The climatic and meteorological factors responsible for changing the suitability and resource availability of a habitat through time may be in large part the same factors that shape the spatial and temporal characteristics of movements from or to that habitat. Climatic changes can influence the spatial distribution of suitable habitats and the absolute resource availability whithin suitable habitats and by doing so influence either directly or indirectly the direction and distance of the movement patterns. Likewise climatic changes can dictate the hetcrogeneity of habitats in time (length of favorable and unfavorable periods, and length of time a location remains suitable) and influence the phenology (timing and rate) of the movements. In the paper that follows I show how the diversity of avian migration strategies can be related to the diversity of environmental changes that occur over different temporal and spatial scales.

## RESOURCE AVAILABILITY, RESOURCE HOLDING POTENTIAL, AND THE PROBABILITY OF MOVING FROM A HABITAT

The level of resource availability in or the favorableness of a suitable habitat can fluctuate greatly. Resource availability can be absolute (the amount of resources in a habitat) or relative (the actual resources available to an individual in relation to other individuals in the population).Absolute resource availability (ARA) is an attribute of the habitat while relative resource availability (RRA) is an attribute of the individual and related to its resource holding potential (RHP). For a given level of absolute resource availability in a habitat, the relative resource availability may be different for each individual in the population. The absolute resource availability within a habitat and the resource holding potential of an individual in a population occupying that habitat, are important in determining the probability that an individual will have to move from the habitat to secure sufficient resources elsewhere. The ARA of a habitat and the RHP of an individual require some additional explanation.

## Absolute Resource Availability (ARA)

The ARA lines in Figure 1 are isoquant lines, each indicating a constant quantity of absolute resource availability in a habitat. The slopes of the isoquant lines are related to the amount of resource encountered as a function of area sampled. Isoquant line $ARA_0$ for example, indicates that no resources are in the habitat. Isoquant lines $ARA_{0.1}$, $ARA_{0.5}$, and $ARA_1$ indicate increasing amounts of resource as a function of area sampled. Isoquant $ARA_\infty$ indicates that resources are infinitely abundant. Although the latter case is unrealistic, it is precisely the same as saying the carrying capacity is unlimited. Thus the series of ARA isoquant lines in Figure 1 illustrate a whole function of the two variables: amount of resource and size of area sampled. Each isoquant is associated with a particular value of absolute resource availability, and the array of isoquant lines represents an isoquant map.

## Resource Holding Potential (RHP)

Individuals in a habitat rarely share resources equally. Given a certain level of absolute resource availability, some individuals acquire more resources than others. In other words, the relative resource availability differs from individual to individual, unless the absolute resource availability in unlimited. The factors responsible for one individual acquiring more resources than another are related to game theory (Maynard Smith, 1976) and the logic of asymmetric contests (Maynard Smith, Parker, 1976). If resources in a habitat are limited, the individuals in a population that occupy that habitat will compete (engage in contests) for access to the resources. Most contests are asymmetrical (Parker, 1974), because individuals vary in fighting ability or resource holding potential (RHP), and the value of the resource to the contestants (expected payoff) often differs. The RHP of an individual depends on a number of factors (e.g., size, age, sex, strength, weaponry, physiological condition, and experience). When the RHP of two individuals are similar a contest may escalate for a brief period until one individual has assessed the RHP of the other. However, in most cases individuals are able to assess asymmetries in RHP without resorting to overt aggressive behavior (Gauthreaux, 1981). In the latter case, the individual with the higher RHP acquires the resource, and the individual with the lower RHP does without and seeks the required resource elsewhere. Consequently, when the absolute amount of resources in a habitat decreases, individuals with relatively high resource holding potential may be able to secure enough resources and remain in the habitat, but other individuals with low RHP's may have to move from the habitat, or perish, because sufficient resources cannot be secured (Baker, 1978, p. 68, 402–406; Gauthreaux, 1978).

The relationship between an individual's resource holding potential and its probability of moving from a habitat is presented graphically in Figure 2. Because this relationship is sensitive to the absolute resource availability in a habitat, the ARA isoquant map of Figure 1 has been included in the graph. The orientation of the isoquant map in Figure 2 is turned 90° counterclockwise relative to Figure 1, because of the convention of having the independent va-
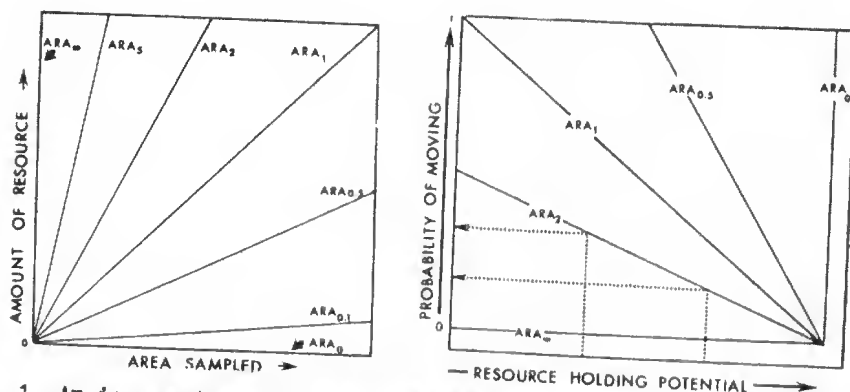
F i g. 1. An isoquant map of absolute resource availability (ARA) in a habitat. Each isoquant line represents all the possible combinations of area sampled and amount of resource found for a particular absolute resource availability

F i g. 2. The graphical relationship between resource holding potential and the probability of moving from a habitat for different absolute resource availabilities (ARA's).

riable (resource holding potential) increase along the abscissa and the dependent variable (probability of moving) increase along the ordinate. The relationships among the isoquants are nonetheless identical to those in Figure

According to Figure 2, when the absolute resource availability of a habitat is unlimited ($ARA_\infty$), all individuals in the population can remain in the habitat regardless of resource holding potential. The area sampled in the habitat to obtain adequate resources can be infinitely small (cf. Fig. 1). This situation is of course unrealistic. As the absolute amount of resources in the habitat declines (isoquant $ARA_2$), individuals with the lowest RHP will have the highest probabilities of moving. When the absolute resource availability is further reduced (isoquant $ARA_{0.5}$), half of the individuals in the population must leave the habitat to secure resources elsewhere. Of the individuals that remain in the habitat, even those with relatively high RHP, must sample large areas to secure sufficient resources (cf. Fig. 1). When the absolute resource availability reaches zero, no individual can remain in the habitat and survive. Thus the amount of resource in a habitat ultimately controls the number of individuals that can stay in the habitat, and the fluctuations in the absolute amount of resource influence the number of individuals that must move from the habitat. With this in mind it is possible to elaborate the various avian migration systems as a function of different temporal fluctuations in the environment.


AVIAN MIGRATION STRATEGIES

Migration in a general sense encompasses all movements in space that an individual makea in response to changes over time (Baker, 1978; Gauthreaux,

1980), including maintenance, dispersal, and migratory movements. In this interpretive overview only the last two types of movement are considered, but maintenance movements (e.g. foraging movements, roosting movements) could be included by emphasizing smaller temporal and spatial scales of environmental change.

The type of movement pattern shown by some or all the individuals in a population depends in large part of the frequency and amplitude of environmental fluctuations that cause variability in the absolute resource availability of a habitat. The variability in the absolute resource availability of a habitat can be attributed to two distinct sources. One source is from processes internal to the habitat that involve interactions of organisms with one another (biomass production and consumption), and the other source is from processes external to the habitat that involve environmental events or changes that are independent of the state of the habitat. Although the internal processes are important and can be evaluated when external processes are more or less constant, the external processes are forcing mechanisms and strongly control internal system variability. Consequently the time scale of external events (environmental changes) favors resonant amplification of internal events (changes in absolute resource availability) on the same time scale, with an appropriate lag. Mitchell (1976) has presented a variance spectrum of climatic variability that spans all time scales of variability from one hour ($10^{-4}$ years) to the age of the Earth ($4 \times 10^9$ years). Three sharp peaks in the relative variance of climate occur at periodicities of 1 day, 1 year, and 100,000 years. These three peaks correspond to the diurnal cycle, annual cycle, and the Quaternary ice-volume cycles. With reference to avian migration systems, the annual climatic cycle has by far the most important influence or internal events within the habitat.

Because of the overwhelming influence of the annual climatic cycle, many habitats show distinct annual periodicities in absolute resource availability. The amplitude of the fluctuations in ARA varies greatly depending on the geographical location of the habitat, and it is the amplitude of the annual fluctuations in absolute resource availability that ultimately influences the migration patterns of birds occupying a particular habitat (Fig. 3).


Breeding and Natal Dispersal

The distribution of a population is inevitably more patchy than the resource distribution, even if the resource distribution itself is random (Roughgarden, 1977). Thus dispersal enhances the chances that an individual with a low RHP in its natal habitat will find a suitable habitat in which to survive and reproduce. Because available habitats are randomly distributed, the orientation of dispersal movements may be random for the population as a whole.

The temporal pattern of dispersal movements is dependent on fluctuations in resource availability over time. Because birds should reproduce when their breeding habitat is at its maximum level of resource availability, dispersal movements occur just prior to breeding (breeding dispersal of adults) or just after breeding (natal dispersal of young). The former move-
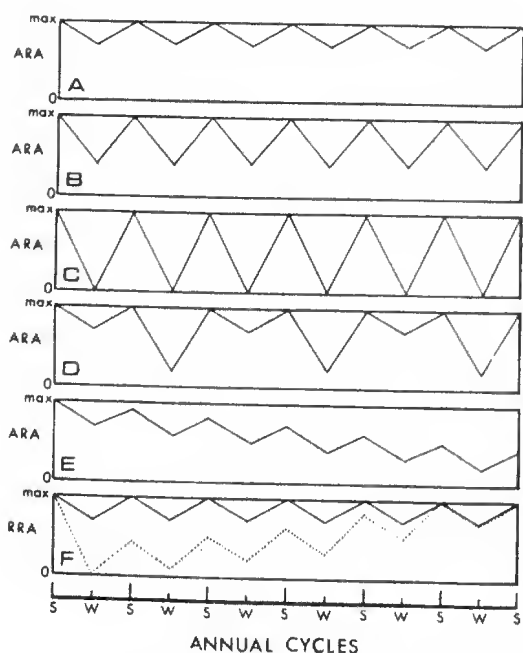
F i g. 3. Patterns of annual fluctuation in the absolute resource availability (ARA) and the relative resource availability (RRA) of a breeding habitat. S - breeding period, W - nonbreeding period. See text for further explanation

ments are spacing processes by which the available habitat is divided among potential claimants, and individuals that have found a place to settle may by their behavior or by their presence alone cause other individuals to look for a settling area elsewhere (Brown, 1975:50). The final distribution of the individuals in the occupied habitat is known as the dispersion pattern of the species (Brown, Orians, 1970). Natal dispersal occurs just after breeding as the level of absolute resource availability begins to decrease in response to increased populations size and the annual climatic cycle (Figure 3A). In birds dispersers are usually young females with comparatively little resource holding potential in their natal habitats (Greenwood, 1980). Through dispersal they may find new habitats where they can avoid intense competitive interactions, secure enough resources to survive, increase their resource holding potential through maturation and experience, and ultimately breed. Once these processes have occurred an individual shows strong site tenacity (reluctance to leave the habitat). Thus once an individual has achieved high resource holding potential, it is unlikely that it will have to leave a habitat or a certain location within a habitat, unless the absolute resource availability declines to levels where survival is in jeopardy. If an individual with high RHP must vacate its breeding habitat (or nonbreeding habitat for that matter) during periods of low or zero ARA, it will likely return to the habitat (show site fidelity) once resource levels increase. For birds, return movements are not characteristic of dispersal, but they are quite typical for migratory movements (Gauthreaux, 1982).

## Partial Migration

When the annual fluctuation in absolute resource availability of a habitat is great, but sufficient resources remain in the habitat during the nonbreed-

624

ing period to permit the survival of a portion of the population, only those individuals with relatively high resource holding potential can remain in the habitat (Figure 3B). Those individuals with lower resource holding potential must move to locations where they'can secure enough resources to survive during the period of low ARA. This pattern of movement is called partial migration, and the individuals that must leave the habitat during the period of low ARA usually return to the habitat from which they departed when the level of ARA increases. Because age and sex are important determinants of resource holding potential, for most species the migrants are young, and in those species where males are dominant to females, the migrants are largely female (Lack, 1954; Gauthreaux, 1978; Greenwood, 1980).


## Complete Migration

When the annual fluctuation in absolute resource availability of a breeding habitat is so great that resource levels reach zero during the nonbreeding period (Figure 3C), no individuals can stay in the breeding habitat and all must move to locations where resource levels permit survival. In this case the distance of movement may be related to the resource holding potential of an individual, such that those individuals with the highest RHP move the shortest distance and those with the lowest RHP move the longest distance (differential migration, but see Ketterson and Nolan, 1982). When all individuals migrate approximately the same distance, RHP may determine the relative quality of the nonbreeding habitat. In both of these cases individuals with the highest RHP would tend to arrive earliest in the breeding habitat once absolute resource levels increase (Gauthreaux, 1978).


## Irruptive Migration and Nomadism

When the annual fluctuation in absolute resource availability of a habitat is different from year-to-year (Figure 3D), the type of movement from the habitat differs from year-to-year. Dispersal movements only may occur during a year with a minor decline in resources, but the following year when resource levels decline sharply, a large portion of the population must leave the habitat to seek resources elsewhere. In the latter case the movement is called irruption (Lack, 1954: 227-242; Bock, Lepthien, 1976), and the individuals that move from the breeding habitat are those with low resource holding potential (Baker, 1978: 634-635). The alternation of movement patterns is coupled with a circumboreally synchronized pattern of seed crop fluctuations in certain high-latitude tree species, and these fluctuations are possibly related to the quasi-biennial cycle of climatic variability (Mitchell, 1976) that is harmonically related to the annual change in climate.

In theory when the absolute resource availability shows strong year-to-year fluctuations in a breeding area, site tenacity should not be adaptive, and nomadism should be a more profitable strategy. This situation has been examined by Andersson (1980), and he concludes that nomadism in birds is a better strategy with cyclic than with random fluctuations in absolute re-

4. Зак. 981

source availability, and the advantage of nomadism increases with the interval between successive good years in an area.

## Biogeographic Migration

Thus far the annual fluctuation in the absolute resource availability of a habitat has been stressed (Figures 3 A-D), but fluctuations in absolute resource availability can and do occur simultaneously over time periods of considerably greater length (longer wave lengths). The latter fluctuations affect not only the absolute resource availability of a habitat but also the nature of the habitat itself through long term successional changes (Figure 3E). Over successive generations the maximum resource availability in a habitat may steadily decline, so that eventually, the habitat is no longer suitable for reproduction. Through annual dispersal movements habitats that are more suitable may be found, and eventually the range of the species will shift so that long term faunal migrations will track long term floral migrations (Gauthreaux, 1980, 1982).

## DIFFERENTIAL MIGRATION AND RELATIVE RESOURCE AVAILABILITY (RRA)

Thus far the emphasis of this paper has been on the absolute resource availability (ARA) within a habitat and how a pattern of decline in ARA influences the pattern of movement of a part or of the whole population from that habitat. In this section I wish to emphasize the relative resource availability (RRA) to an individual and how this may influence the migration strategy of that individual. The relative resource availability is that portion of the absolute resource availability within a habitat available to an individual because of its resource holding potential relative to that of other individuals occupying the habitat or location (Figure 3F). Even when the absolute resource availability within a habitat is high, for an individual with relatively low resource holding potential, relative resource availability is low. Figure 3F illustrates the relative resource availability (RRA) to an adult and to a young bird of the year over successive annual climatic cycles. During the first nonbreeding period (W) the RRA declines only slightly for the adult, but for the young of the year the RRA declines sharply. During subsequent breeding and nonbreeding periods the difference in RRA between the adult and the maturing immature decreases, so that after several annual cycles, no difference exists. This pattern is fundamentally similar to that found in a number of seabird species (Dunnet et al., 1979). The pattern can apply to other species as well (e.g., Gannet _Sula bassana_, White Stork _Ciconia ciconia_, Osprey _Pandion haliaetus_, Manx Shearwaters _Puffinus puffinus_), but depending on the species, the number of annual cycles needed before an individual acquires a high resource holding potential and hence a high relative resource availability will be less.

The spatial extent of movements of individuals from a breeding location are manifestations of the differences in relative resource availability at the breeding location. For many bird species during the nonbreeding season the youngest individuals in the population are distributed the farthest away

626

F i g. 4. The age dependent migration distances of Harring Gulls in relation to monthly climatic changes (modified from Moore, 1976)
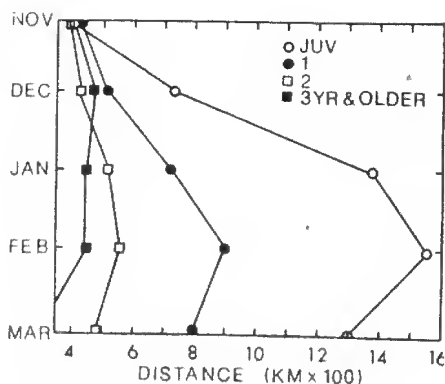
from the breeding location and the adults are closest to the breeding location. The distance from the breeding location that an individual overwinters is determined by its resource holding potential in relation to the absolute resource availability of a location such that it will have a high relative resource availability for survival. Even though an individual may have a low resource holding potential, if it can find a suitable habitat with few or no individuals with higher resource holding potential, it will enjoy a relatively high resource availability and be able to survive. Thus individuals with high resource holding potential can move relatively short distances from breeding locations (or not at all) and secure sufficient resources for survival during periods of reduced absolute resource availability, but individuals with low resource holding potential may have to move considerable distances before they can find a location where the relative resource availability is high enough for survival. The data in Figure 4 are

from a month-by-month analysis of banding returns of Herring Gulls Larus argentatus from the Great Lakes of the United States (Moore, 1976). In November when climatic conditions are still relatively mild, all age classes are recovered near the breeding grounds. As winter progresses, the age classes show greater segregation with maximum segregation occurring in early February. Once climatic conditions improve in March all age classes move toward the breeding grounds, because the amount of absolute resource availability within the breeding areas is increasing. The axis of movement should generally follow the climatic gradient and be perpendicular to the isotherms, because of the relationship between the severity of climate and absolute resource availability.

CONCLUSIONS

The amount of resource in a habitat ultimately controls the number of individuals that can stay in the habitat, but the fluctuations in the amount of resource influence the number of individuals that must move from the habitat. Thus, the spatial movements of birds, whether maintenance, dispersal, or migratory, are evolutionary strategies that express the expectation of temporal changes in conditions at the present locality. It is the nature of the

temporal changes that dictates the type of spatial movement that an individual will show.

Temporal changes in resources can be attributed to processes within the habitat (resource production and consumption, habitat-organism feedback) and to processes outside of the habitat that involve environmental changes that are independent of the state of the habitat. Because external processes are forcing mechanisms, the time scale of external events (environmental changes) favors resonant amplification of internal events (changes in absolute resource availability and all the covaring biological events) on the same time scale with an appropriate lag. Thus, habitats may fluctuate asynchronously in favorableness or absolute resource availability because of stochastic biological events (different population levels in different habitats), but synchronous changes in favorableness or absolute resource availability may also be superimposed on these habitats by widespread, deterministic climatic events (daily and annual climatic cycles).

When habitats fluctuate in favorableness asynchronously, a dispersal strategy will be adaptive, but when synchronous fluctuations in favorableness occur, a migration strategy will be adaptive. The type of migration pattern (partial, irruptive, short- or long-distance) shown by a species will depend on the amount of decrease in the absolute resource availability within the habitat. The individuals that stay (if any) and the individuals that leave during periods of reduced resource availability within the habitat will depend on certain attributes of the individual and the absolute resource availability within the habitat. The individuals with high resource holding potential and high dominance status will perceive high relative resource availability and will be able to remain in a habitat with low absolute resource availability. Those individuals in the population with low resource holding potential (and consequently experiencing no relative resource availability) will have to move as far as necessary to locate a habitat where they too can experience a relative resource availability that will permit survival.

Although differences in the resource holding potential of the individuals in a population have been emphasized as being important proximal factors in the incidence of migration, the same factors may be applied to differences in migratory behavior between species. O'Connor (1981) has shown that migrant-resident differences are significantly related to body size differences, such that the larger species show a high competitive ability to exploit resources during the breeding season and that the smaller migrant species are primarily exploiters of breeding season resources under-exploited by a resident population held down by winter mortality (see also Herrera, 1978). Thus, asymmetries in RHP such as size may be as important to species differences in migration as it is to individual differences in migration.


SUMMARY

Climatic changes can control the spatial distribution and relative favorability of suitable habitats and by doing so influence either directly or indirectly the direction and distance of the movement patterns. Likewise climatic changes can dictate the heterogeneity of habitats in time (length

of favorable and unfavorable periods, and length of time a location remains suitable) and influence the phenology (timing and rate) of the movements. Thus by tracking climatic and meteorological changes through movement, birds can maximize the expectancy of finding a new suitable habitat or returning to a suitable habitat after a period of unfavorability. Depending on the rate and nature of environmental changes and the life span of the individuals, several types of "migration" patterns can be realized (e.g., zoogeographical migrations mediated through dispersal, partial migrations, irruptive movements, and short- and long-distance seasonal migrations). The diversity of avian migration strategies can be related to the diversity of environmental changes that occur over different temporal and spatial scales.

R e f e r e n c e s

Andersson M. -J. Anim. Ecol., 1980, 49, p. 175-184.
Baker R.R. The Evolutionary Ecology of Animal Migration. N.Y.: Holmes and Meir, Inc., 1978.
Bock C.E., Lepthien L.W. - Amer. Nat., 1976, 110, p. 559-571.
Brown J.L. The Evolution of Behavior. N.Y.: Norton, 1975.
Brown J.L., Orians G.H. - Ann. Rev. Ecol. and Syst., 1970, 1, p. 239-262.
Dunnet G.M., Ollason J.C., Andersson A. - Ibis, 1979, 121, p. 293-300.
Gauthreaux S.A. Jr. - In: Perspectives in Ethology. Vol. 3 / Eds. P.G.Dateson, P.H.Klopfer. N.Y.: Plenum Press, 1978, p. 17-54.
Gauthreaux S.A. Jr. - In: Animal Migration, Orientation, and Navigation / Ed. by S.A.Gauthreaux, Jr. N.Y.: Academic Press, 1980, p. 103-174.
Gauthreaux S.A. Jr. - Behavioral and Brain Sciences, 1981, 4 (3), p. 441.
Gauthreaux S.A. Jr. - In: Avian Biology. Vol. 6 / Eds. D.S.Farner, J.R.King, K.C.Parkes. N.Y.: Academic Press, 1982.
Greenwood P.J. - Anim. Behav., 1980, 28, p. 1140-1162.
Herrera C.M. - Auk, 1978, 95, p. 496-509.
Ketterson E.D., Nolan V., Jr. - Auk, 1982, 99, p. 243-259.
Lack D. The Natural Regulation of Animal Numbers. Oxford: Clarendon Press, 1954.
Maynard S.J. - Amer. Sci., 1976, 64, p. 41-45.
Maynard S.J., Parker G.A. - Anim. Behav., 1976, 24, p. 159-175.
Mitchell J. Jr. - Quaternary Res., 1976, 6, p. 481-493.
Moore F.R. - Bird-Banding, 1976, 47, p. 141-159.
O'Connor R.J. - In: Animal Migration / Ed. by D.J.Aidley. Cambridge: Cambridge Univ. Press, 1981, p. 167-195.
Parker G.A. -J. Theor. Biol., 1974, 47, p. 223-243.
Roughgarden J. - Oikos, 1977, 29, p. 52-59.

# WHY DO BIRDS MIGRATE? INTER AND INTRASPECIFIC COMPETITION IN THE EVOLUTION OF BIRD MIGRATION
## CONTRIBUTIONS FROM POPULATION ECOLOGY

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There are several proposed reasons why birds migrate. The most widely accepted, according to a recent, excellent review by Gauthreaux, is that bird migration is an adaptive response to changing environmental conditions,and/or changing biological needs (e.g. between reproductive and non-reproductive seasons). I accept this basic explanation as my starting point, and go on to consider specifically which of all the possible changes that birds face in an annual cycle are most important in causing or maintaining migration.

## FORMAL STATEMENT OF THE ADAPTIVE MIGRATION HYPOTHESIS

First, we will consider the migratory habit as an Evolutionary Stable Strategy as defined by. Maynard-Smith. Thus, we consider how natural selection works to maintain the migratory habit. We suppose that individuals in the migratory population vary in their propensity to migrate (for example, in distance covered), but that extreme deviations (such as a bird that migrates only half of the way to the breeding or wintering grounds, landing outside the normal range of the species) are simply unsuccessful in survival and reproduction, and are eliminated from the population. With them are eliminated any factors (especially genetic factors) that led them to make their deviate migration. Then bird species that migrate keep on migrating because individuals that do not carry out a normal migration are selectively eliminated.

An alternative way of viewing this hypothesis supposes that if the population ever did exist as a resident population in either the non-breeding or the breeding grounds, then extreme deviations from this pattern of residency which led individuals to migrate according to presently existing habits would be selected for. That is, if the population were residents, any individuals which migrated would have a higher survival or reproduction and so would increase in representation in the population. Since this argument assumes that such "extreme deviations" would occur in both populations, and would (at least sometimes) have a genetic basis so that it could be passed on to later generations, it follows that:

1. Natural selection against such deviates maintains existing migratory habits.

2. Natural selection for deviates resulted in the development of existing migratory habits.

## DEVELOPING TESTS OF THE ADAPTIVE MIGRATION HYPOTHESIS
## WHY DO BIRDS FAIL TO SURVIVE AND REPRODUCE?

In order to test the adaptive migration hypothesis, we will benefit from having some idea about what causes migrant birds to be less successful when they migrate in an extremely different way from present patterns (or fail to

migrate at all). This is a matter explored in a different area of ornithology, namely that part concerned with the regulation of population by the balance of birth and death rates. I offer the following questions and answers.

1. Question: Why are birds nesting in some places more successful in raising young that birds nesting in other places?

Answer: The major factor affecting reproduction for most land-bird species is nest predation. Food supply is also involved, but appears to be of only minor importance since predictions based on the hypothesis that food supply is limiting are not as generally confirmed. According to studies by Skutch and Lack, nest predation varies substantially (from 90% on small open nesting species in the tropics, to 0% in some hole nesting species in boreal regions). Predation is usually rather high (a review by Nice indicated 50% or more for most species in regions with high densities of species). I and others have shown it to be density dependent. Curiously, nest predation also seems to be a good correlate with other variables that affect production, such as clutch size. Clutch size in birds varies as much or more than predation, and seems at first to reflect the importance of food supply to breeding birds. However, there are few clear demonstrations that food supply affects clutch size to a degree necessary to explain the great variations in the variable. While birds sometimes do lay extra eggs when food supply is especially high, huge increases or variations in food supply usually lead to only minor increases in clutch. Only some arctic, predacious birds show a remarkable increase in clutch with an abundance of food.

However, predation correlates very well (inversely) with clutch size. Skutch's data show that in the tropics, species with nests experiencing 90% predation rates often lay only one or two eggs, while other species, with similar feeding habits, breeding in the same forest, at the same time, but which only experience 60%-70% predation, because they nest in protected sites, have twice the clutch size. Nice shows that this holds in temperate regions as well, where hole-nesting species have half the predation and twice the clutch of open-nesting species. One interesting comparison clearly suggests to me that predation might be a causative variable affecting clutch size. In central Kansas, Loggerhead Shrikes (<u>Lanius ludovicianus</u>) and Eastern Meadowlarks (<u>Sturnella magna</u>) breed together in prairies dotted with scattered thorn trees and cedars. The birds are the same size, feed on similar (often identical) prey (but in different manners), and nest at about the same time. The meadowlarks nest on the ground, and dome over their nests so that they are quite well protected from the elements, and might be thought to be similar to a hole-nesting species. The shrikes nest up in the shrubs, and have an open nest. However, the meadowlarks suffer high predation rates (60% or so) and only lay three to five eggs per clutch. The shrikes have a low predation rate (20%) and lay six to eight eggs per clutch.

Another interesting note about clutch sizes is that there are cases where they don't vary. Shorebirds (<u>Charadriiformes</u>) almost all lay four eggs, although the great diversity of feeding methods and the wide geographic and habitat ranges occupied would surely imply huge differences in food resources.

Someone needs to examine variation in nest and young predation in these species to see whether it varies as substantially as food supply.

These observations do not exclude food as an important variable generally affecting nesting success, but they do lead us to place most emphasis on nest protection.

2. Question: Why do birds living in some places (e.g. the tropics) have higher survival rates during non-breeding seasons than birds living in other places (e.g. boreal zones)?

Answer: Tropical temperate patterns in annual survival at first seem attributable to climatic variations, since weather is much more extreme and harsh in high latitude zones. However, I regard as more plausible a rather more complicated alternative involving food limitation.

Food resources are now known to vary in their defensibility, so that species consuming limited, defensible resources will set up contests to decide who will feed and who will store. Other species will be unable to set up such contests, and the competition for food will be a "scramble". In the first case, the winners of the contests have a very high survival rate, while the losers have a very low survival rate. Since the losers are lost so quickly, mostly winners are studied by the biologists who consequently record that such species have higher survival rates. Scramble competitors have near equal rates of survival for most members of the population, which are consequently, on the average, lower than the rates for winners among contest competitors. It seems likely that tropical species, for example, have low reproductive rates (due to high predation rates on nests) plus a stable environment, which leads both to fewer competitors and more easily defended territories. As a result, the survival of adult, territory holders is high. Temperate species produce more young, which makes defense of resources by the older generation against the younger more difficult. Also, the instability of the environment makes defense more difficult, so that adults cannot be such "winners" and have to "scramble" more for resources. When resources get low, all "scramblers" suffer equally, and so survival is lower.

The simpler answer, that the rate of climatic accidents varies from place to place, according to the variability in the environment, naturally is preferable, according to Occhams razor. It is also rather plausible, since birds that move about a lot experience more "accidents" (including predation that results from a bird being in an unfamilair setting), and cold weather in itself is a threat.

However, Kluyver has experimentally shown that a reduction in scramble competitors in temperate regions significantly increases the survival rate of dominant individuals. Also, survival rates do not increase with age past the time when a young bird starts breeding (Lack, 1954) which is not what one would expect given that learning to avoid accidents is important. The temperate climate does vary in a fairly predictable way, and one would suppose that a seven-year-old resident Parid in a temperate region would be more familiar with its circumstances.

So, there are experimental data supporting the more complex competition-for-food idea.

Thus, we have from avian population ecology some fairly plausible suggestions as to why a deviant migrant might fail to be successful. A wintering bird of a tropical-temperate migrant species, which failed to migrate, but which instead stayed to breed in the wintering area, would produce far fewer young than its conspecifics, even if mating problems were solved, because its nests would be taken by predators. During the next winters, while it might be quite dominant and established on the wintering grounds, the flood of young birds produced by the migrants would create such scramble competition, that the resident deviant would likely die before it had (finally) reared a successful brood to replace itself.

In a tropical-temperate migrant species, a bird which had bred in a temperate zone habitat, but which then failed to leave in winter, would become a temperate resident. This bird would probably fail to survive the winter, not because of cold per se, or climate, but because it would either not find enough to eat or it would be so harassed by dominants of other species that it would succumb.

Thus, variations in nest predation in the breeding season and food limitation in winter might maintain existing migratory patterns, at least for land birds.


HOW, THEN, DID MIGRATION EVOLVE? SOME SCENARIOS...

Before considering these scenarios, we need to note an asymmetry between winter limitation by food and breeding limitation by nest predation. While both are density dependent, there is a greater potential for community effects in nest predation than there is for food. Nest predation becomes density dependent because a higher density of nests results in more successful predators, which, in turn, leads to greater predation pressure in the region of the nest. Most nest predators (snakes, jays, weasels), have generalized broad diets, including all sorts of prey besides birds nests, which they only specialize on when they chance upon a high density. As a result, when one species is dense, it attracts predators to most other species nesting with it. This means that competition is extremely diffuse in the community and each species' success is highly dependent on the overall community density.

Competition for winter food, however, commonly allows more specialization, especially in stressful times. Newton, for example, showed that wintering Eriorillidae ate entirely different kind of foods during the coldest parts of winter. Thus, most species seem to have some resources that they and they alone feed on, due to morphological, or behavioral adaptations. Such species, while being affected by overall community levels, also seem to have a base level related to an independent resource that is less, or not, affected by the overall community density.

Now, consider a tropical resident population evolving migration. Such a resident species might have a deviant individual (and its mate), which left to breed at some higher latitude where, for some reason, there is less predation on nests. This individual would produce more young than if it had stayed to breed with its conspecifics, but might suffer a loss in survival due to difficulties in regaining a territory among the resident birds. Howe-

ver, they might produce enough more young to overcome any loss in survival the family may have incurred in the ability to control resources by contests. Then their numbers would increase, and eventually would put such pressure on winter resources that overall survival would drop, and only migrant types would be able to replace themselves. The residents would decline. This decline would not raise survival rates, because the migrants would take up the slack. Nor would it raise nesting success rates, since the species, being only a small part of the tropical breeding community would not much affect the overall breeding density, or its nest predation rate. So, the residents would go extinct.

Species resident in the tropics which have not evolved extensive contest competition because of flocking, erratic movements, intense predation on displaying individuals, or indefensible resources, would obviously be more likely to have migrating deviants come home with enough extra young to overcome their dominance disadvantage. In these species, contest competion is not so important, so that a complete migration habit could readily evolve.

A temperate resident species evolving migration to the tropics would send deviates to winter at lower latitudes, where the overall survival rates are higher that the survival of the resident population in the temperate zone.

However, it is a bit difficult to see how such migrant individuals could invade a tropical community successfully, if indeed competition for food is as critical as we expect and is commonly mediated through contests.

There are few ways a bird from a temperate community could take advantage of the apparently higher survival rates in tropical communities if the higher survival rates are generally associated with being the winners in a competitive contest. The migrants, it seems, would normally lose such contests.

However, if a temperate resident had a deviant migrant to the tropics, and if it did survive better than its peers which were maintaining their residency, then it could return with greater probability, and a normal breeding success would result in a population increase for its genotype. It would increase, until nesting success in the temperate habitat was reduced, and the residents would find their survival inadequate to keep their numbers up. Then the residents would decline.

Note, however, that in this case it is unlikely that the residents' population could be driven to extinction, since, as the residents declined, their winter food would increase and also their survival. Thus, some remnant of the resident population would remain. In the case of the tropical resident evolving into a migrant species, as long as the increase in nesting success enjoyed by the migrants outweighed the benefits of contest competition enjoyed by the residents, the migrants will steadily increase and drive the residents to extinction. The migrants, by steadily increasing, steadily increase the scramble competition, which lowers the survival of every member of their species. The tropical residents, however, because nest mortality responds to total species community density and not to individual species density, would find little or no increase in their nest success as they got rarer. They would just be outcompeted, and the whole resident genotype would become extinct.

Thus, scramble competitors moving to higher latitudes to breed are able to

take advantage of the greater reproductive rates there, while such species moving to lower latitudes to winter will be unable to enjoy the higher survival rates there. The higher reproductive rates are available to all species and individuals; the higher survival rates are available only to the winners of competitive contests which normally are established residents.

These scenarios produce a significant conclusion. If the hypotheses from population ecology are confirmed, and if the idea of adaptive migration is true, then the evolution of tropical-temperate migrants from tropical species is likely, but the evolution of such migrants from temperate species is unlikely. The evolution of equator-ward migrating species from temperate species can occur, but it is most likely to involve partial migrants moving into niches where contest competition is minimal (e.g. disturbed habitats). The individual migrants which leave such populations will likely be subordinants with low potential survival in the temperate region of residency.

Let me summarize the prediction from these scenarios:

1. In general, there ought to be a correlation between contest and scramble competition in winter, and migration habit, so that scramble competitors migrate more frequently(Fig. 1).

2. Tropical resident species in indefensible non-breeding season niches will evolve complete temperate-tropical migrants. Temperate resident species will either not evolve temperate-tropical migrants, or will evolve incomplete migration systems(Fig. 2).

3. In migrant species, deviants tending towards residency from normal migration patterns will result in wintering individuals with lower survival, or breeding individuals with increased nest predation(Fig. 3).

I close by making some observations that challenge this perspective on migration. There are many cases in North American birds where one species replaces another in their migrations. For example, the Hermit Thrush (Catharus guttatus) winters in the Southeastern U.S., and migrates to the Northern U.S. and Canada to breed. It is replaced in summer over most of its wintering range by the Wood Thrush (Hylocichla mustelina), which winters in South America. If it is advantageous for a thrush to migrate from the Southeast to Canada to breed, why does the Wood Thrush not keep on migrating and join the Hermit Thrush? And, if it is not advantageous, why does the Hermit Thrush leave?

There are many cases like this. Winter Wrens (T.troglodytes) winter in the central U.S. where House Wrens (T.acdon) breed, but do not winter. Yellow-throated Warblers (Dendroica dominica) only breed in southeastern pine forests where Yellow-rumped Warblers (D.coronata) only winter. The simple explanation that tempts us is that these birds are seeking a uniform climate, and are migrating to keep from adapting physiologically to the extremes they would experience if they were residents. However, if such climatic adaptation were important, one would expect, say, Bergman's Law to apply. However, the Wood Thrush is larger than the Hermit Thrush, and the House Wren is larger than the Winter Wren. Thus, the cold-climate species is smaller, not larger.
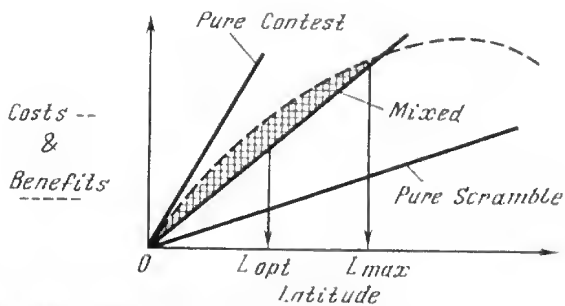
F i g. 1. Costs and Benefits of migration

The costs (solid lines) and benefits of migration are shown, plotted against latitude, with the origin being the wintering grounds. The costs, in increased death rates, stem from two sources: the costs of actually travelling, which increase with distance traveled, and the costs of reduced contest-competitive ability on the wintering grounds. The benefits increase with latitude, but at a diminishing rate, and would actually decrease at very high latitudes. The intersection of costs and benefits set an upper limit ($L_{max}$) to the latitude it would be advantageous to migrate to, but the difference between benefits and costs (hatched area) reaches a maximum at $L_{opt}$, and this determines the best latitude a migrant might achieve. Species which invest heavily in contest competition always pay more than they gain when they migrate, and so will always be resident ($L_{opt} = 0$). Species which have no contest competition will migrate to rather high latitudes, since the only costs they pay are those of travelling. Mixed contest-scramble competitors would stop at lower latitudes
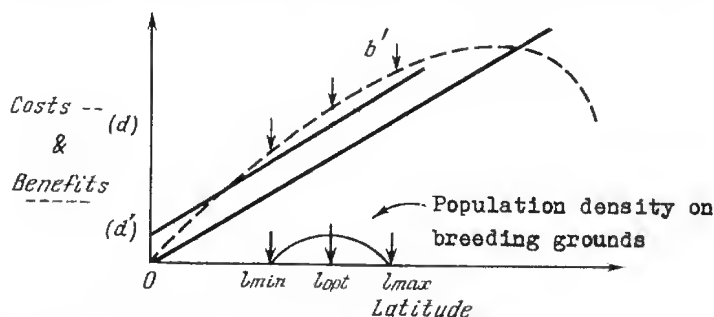
F i g. 2. Population consequences of migration

The migratory habit will increase the population size on both the wintering and the new breeding grounds, increasing death rates (costs) d', and decreasing birth rates b', until b=d between $l_{min}$ and $l_{max}$. Because the difference between benefits and costs will be greatest at $l_{opt}$, the greatest breeding population will occur there, before benefits are reduced to equal costs

At present, I am working on a model for migration strategy which predicts the extent of migration for differing levels of contest and scramble competition. My work so far draws on the idea that not only does the kind of competition affect whether or not a species migrates, but also affects how far

636
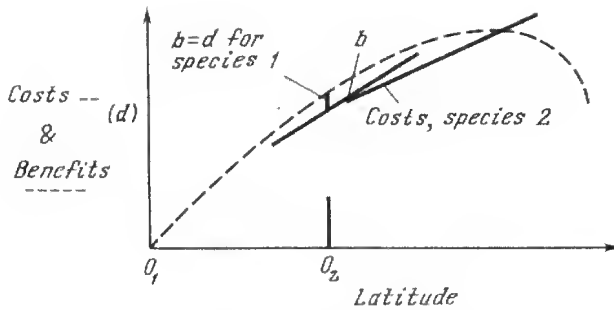
F i g. 3. Competition between a migrant into a region, and a resident species already  there

From the previous figure, the migrant into a region lowers the birth rate there by b', causing residents in that region to lower their populations until their birth rate equals their death rate. The benefits-costs curves for these other species (2) are shown, similar to those of Fig.1, with the origin displaced to the higher latitude where they are resident ($O_2$). Other species (2) with a lesser investment in contest competition, and, hence, a lower slope to their costs curve, will find it advantageous to migrate even further north

it goes. The model suggests that the Wood Thrush and House Wren are more contest competitors than the Hermit Thrush and Winter Wren, and that the benefits of migrating within the temperate zone do not outweight the costs for the former species, but do for the latter. Also, the northern species may have been forced into migration by the invasion of their breeding grounds by the more southern species, which would lower reproductive rates there. The larger size of the southern species is interpreted as a reflection of their greater investment in contest competition.

Of course, these speculations need to be developed so that predictions are generated and tested before they can be regarded as very plausible.

SUMMARY

Two contrasting hypotheses explaining why some birds migrate and others do not involve competition and physiological flexibility. The competition hypothesis argues that fluctuations in community carrying capacity force some birds to leave areas where they bred to winter elsewhere, and some to leave areas where they winter to breed elsewhere. The physiological flexibility hypothesis argues that some birds develop narrow physiological requirements but high efficiencies, and migrate to keep in a constant environment, while other birds develop flexible physiological requirements, trading off efficiency, to take advantage of a broader niche.

In this report, I develop the competition hypothesis to the point that it can be readily tested, and offer several tests of predictions. I conclude that while most temperate bird species are winter limited, competition for nesting sites, both intra and interspecifically, is the major selective force behind migration.
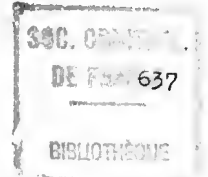
# HABITAT PHENOLOGY AND SPRING MIGRATION SCHEDULES

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## INTRODUCTION

Most temperate species of birds live in seasonal fluctuating environments, subject to annual changes in climate and photoperiod, and in food quality and quantity. The birds have developed a timing programme which adjust the onset of important events, such as migration, breeding and the moult, to the most favourable periods of the year. The reproductive cycle exihibits the greatest degree of environmental dependence. Migrant birds therefore have to time their return to their breeding areas in spring so as to be able to utilize to the full the spring flush of food, for reproduction. A balance exists between opposing selection pressures: firstly, selection for as early an arrival as possible, because this will increase their chances of occupying an optimal breeding territory and nest site and of getting a mate (von Haartman, 1968). This is probably the reason why the males of many species return before the females (Schüz, 1971); secondly, the opportunity for early breeding, which seems to be favourable for the raising of more offspring, of larger broods, and of several successive broods, increases the survival rate of the juveniles and allows more time for the preparations for the autumn migration (Perrins, 1970; Mac-Lean, Pitelka, 1971; Hussell, 1972; Sokolov, 1975). Early departure also helps to minimize the competition for food in their wintering areas (Lack, 1968). On the other hand, there is a concomitant risk of the renewed onset of low temperatures, rain and snowfall later in spring which may greatly reduce the availability of food, with widespread bird mortality in consequence (Nisbet, Drury, 1968; Sealy, 1975; Ojanen, 1979). An early arrival to the breeding grounds may also involve a depletion of those stored food reserves which should have been available for reproduction, e.g. for egg production by the females. A relationship seems to exist, for instance, between clutch size and the condition of the females on their arrival in spring (Picula, 1976; Silverin, 1981).

In studies of bird migration much attention has been paid to the factors underlying the start of the migration from the winter quarters and also to those which stimulate or suppress the rate of migration itself; e.g. such factors as physiological changes induced by day-length variation, weather conditions and food availability. Few studies have been paid to the variation in the arrival times of birds in relation to the environmental conditions which they encounter on arrival. In the present paper I shall concentrate attention on the latter subject.

## ENVIRONMENTAL VARIABILITY AND BIRD ARRIVAL AND BREEDING TIMES

In temperate and arctic regions plants grow and fruit only at certain times of the year, and the biomass of invertebrates also changes seasonally (Danilevskii, 1965; Bradshaw, 1974; Lieth, 1974). In addition, these phenophases are subject to annual displacement in different geographical areas due to fluctuations in the physical environment.

According to the "bioclimatic law" of Hopkins (1938) there is a general retardation in season of four days for each degree of northern latitude in the

northern hemisphere, for every five degrees of eastward longitude across a
continent, and for every 100-125 m of altitude. One would therefore expect
to find that bird breeding times will be displaced in a similar manner (Im-
melmann, 1971). This does not, however, seem to be true. Baker (1938) conc-
luded that there is a general tendency for the egg-laying season, for all
kinds of birds, to start later and later the further north one goes, to the
extent of some 2-3 days per degree of northern latitude (1.8 days for passe-
rines). The culmination of the egg-laying season in general is only retarded
by about 1.4 days per degree of latitude. The latitudinal retardation in the
breeding times of passerine birds in Fennoscandia also seems to be less than
that of the developmental stages of the vegetation (Slagsvold, 1975, 1977),
although exeptions are found (Slagsvold, 1975, 1976a). Observations on the
timing of the annual phenophases of different plants (time of leafing,flower-
ing and fruiting), i.e. phenology, enjoys a long tradition among botanists
in many countries, as also observation of the arrival dates of the different
birds from their spring migration does among ornithologists. However, the in-
terrelationships of these two types of phenological studies have seldom been
studied. I have made such a study of the phenological data for Norway, and
came to the conclusion that the latitudinal and altitudinal retardation in
the arrival dates of birds is less than the retardation in the developmental
stages of the vegetation (Figs. 1, 2, 3); viz. only about 6 days in arrival
time for every 10 days retardation in vegetational development (Slagsvold,
1976b). The development stages of invertebrates are also closely related to
the environmental temperature and to the stages of vegetational development.
Thus, the latitudinal retardation in the arrival times of the birds would
also seem to be less than the equivalent retardation in the timing of the va-
rious phenophases of the invertebrate fauna in the same areas (Slagsvold,
1976b, 1977). It should be noted that the northward progression in the dates
of the first appearances of birds is far less than that which is theoretical-
ly possible, based on recorded flight speeds (von Haartman, 1956; Salomonson,
1967), and that the arrival times on their breeding area are not directly re-
lated to the actual distance travelled (Stresemann, 1948), although there is
a tendency for the winter ranges of late-returning species to lie further
south (Hemmingsen, 1951; Weydemeyer, 1973).

As seen from Fig. 2, the phenophases of the plants which start growing
early on in the year are more retarded than those which commence growth la-
ter, and that such a tendency also holds true for the arrival dates of the
birds studied. Although the arrival dates of the majority of the bird species
in the Norwegian study showed less latitudinal retardation than that found
for the phenophases of the plants, exceptions were found, particularly among
"early" arrival birds such as the Thrush Turdus species. In Finland, for in-
stance, the spring arrival of the Song Thrush Turdus philomelos is said to
follow the 0° isotherm, which is about two weeks before the local snowmelt
commences (Siivonen, 1939). The time of the snowmelt probably represents the
primary limitation to the possible arrival times of many early-arriving spe-
cies of birds (Stresemann, 1948; von Haartman, 1956; Irving, 1960; Pikula,
1971; Slagsvold, 1977; Mikkonen, 1981a,b), although in Sweden the Skylark
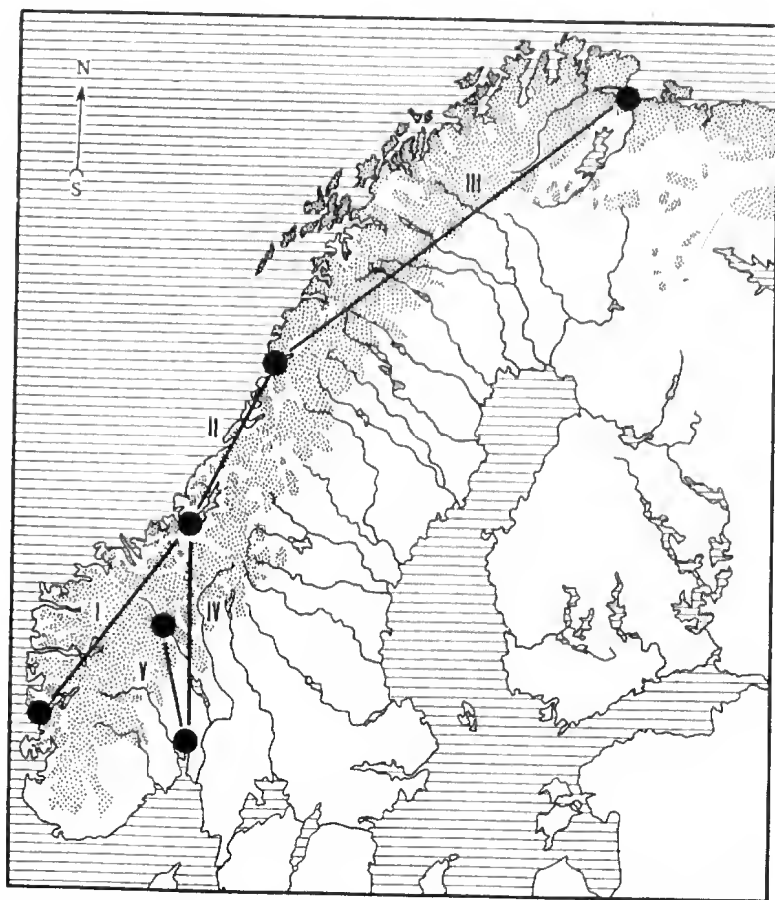Alauda arvensis has been reported as arriving contemporaneously in localities

F i g. 1. Five gradients in Norway for which bird arrival dates and dates of plant phenophases have been compared

with different snow-depths (Wallentinus, 1970). The arrival of birds of prey is not dependent upon the existence of snow-free areas, whereas the breakup of ice cover is a prime factor determining the arrival times of aquatic migrants (Irving, 1960; Wallentinus, 1970; Väisänen, 1974).

The arrival of those bird species which normally return late is not only less retarded in relation to increasing northern latitude and altitude than those which return early, they are also subject to less annual variation.This holds true both in the south and in the north of Norway (Fig. 4), and is a well-known phenomenon (e.g. Wallentinus, 1970; Weidemeyer, 1973). The arrival times of the "early" species have been found to be more influenced by the weather conditions, by the ambient air temperature in particular (Salomonsen, 1967; Schüz, 1971; Weidemeyer, 1973). Such "early" species may even reverse their migration direction in bad weather. The arrival times are not only dependent upon the environmental conditions prevailing in the breeding areas on arrival, but are also related to those in the areas traversed during the spring migration and to those which have prevailed in the species' winter quarters. In late spring the air temperature is generally higher, and the birds may be
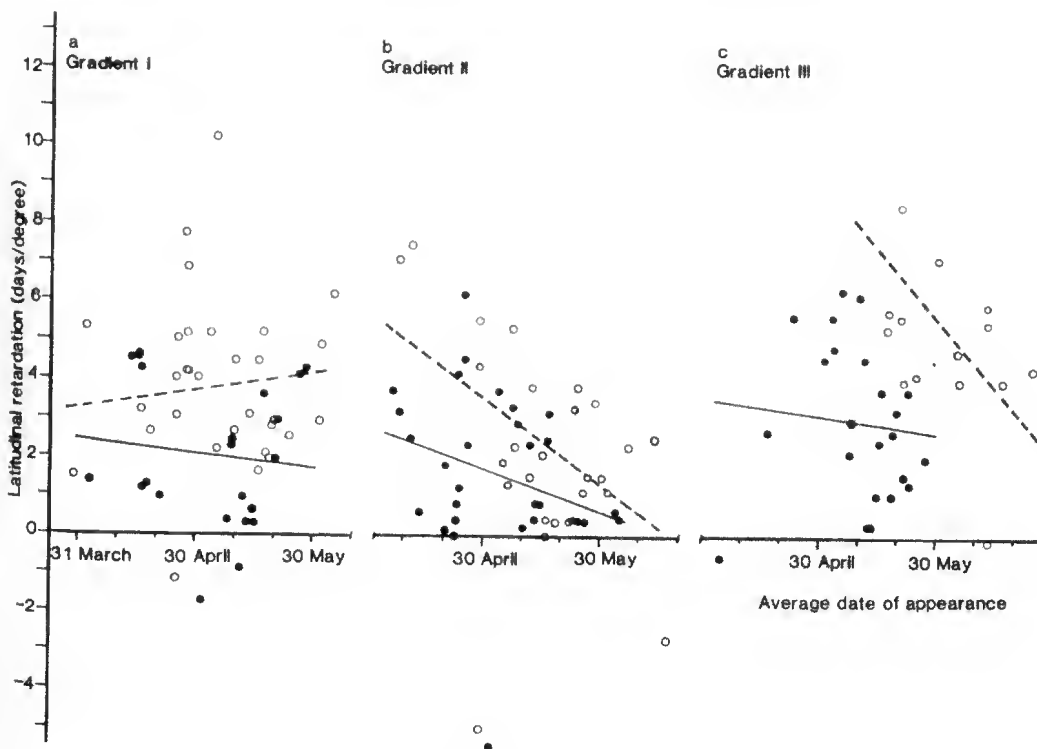
F i g. 2. Comparison of the latitudinal retadatioo in the arrival dates of birds during the spring migration (closed circles) and io plant pheoopha-ses (opeo circles) along the coast of Norway. The gradients referred to are those indicated io Fig.1. The respective regression lines are added, a solid line for bird arrivals and a dashed line for plaot phenophases (from Slagsvold, 1976b)

less susceptible to fluctuating temperatures while on migration (Slagsvold, 1976b).

The time elapsing between arrival and egg-laying is hort in "late" seasons and at high latitudes and altitudes, as well as for late arriving birds (Slagsvold, 1975, 1976b, 1977). For a late-arriving specics, the Pied Flycatcher Ficedula hypoleuca, not only is a low correlation between arrival time and habitat phenology typically recorded (von Haartman, 1956), but also a rather low correlation between the time of appearance of the first birds to arrive in the spring and the onset of egg-laying, in particular at high latitudes (Slagsvold, 1976a). The males of this species arrive before the females, and it is the arrival time of the latter, of course, which determincs the onset of breeding. It is noteworthy that whereas the annual variation in the date of the onset of egg-laying by the Pied Flycatcher in Finland is only slightly correlated with the ambient air temperature and habitat phenology, it is closely correlated with the onset of egg-laying, and thus of female arrival, much further south, viz. in Dresden in · GDR (Slagsvold, 1976a). In comparison, the time of egg-laying by those bird species which arrive early (the "weather migrants") seems to be much more closely correlated with habitat phenology and
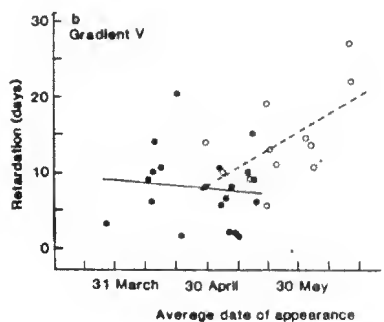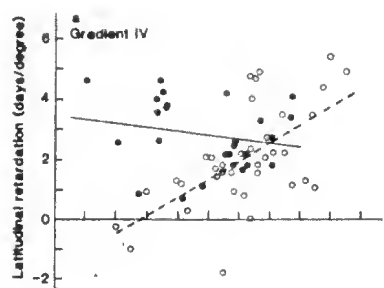
F i g. 3  is for Fig. 2, but in b the plain interval in days between the respective events is used, without being previously divided by the difference in latitude, because altitudinal differences also exist between areas (from Slagsvold, 1976b)
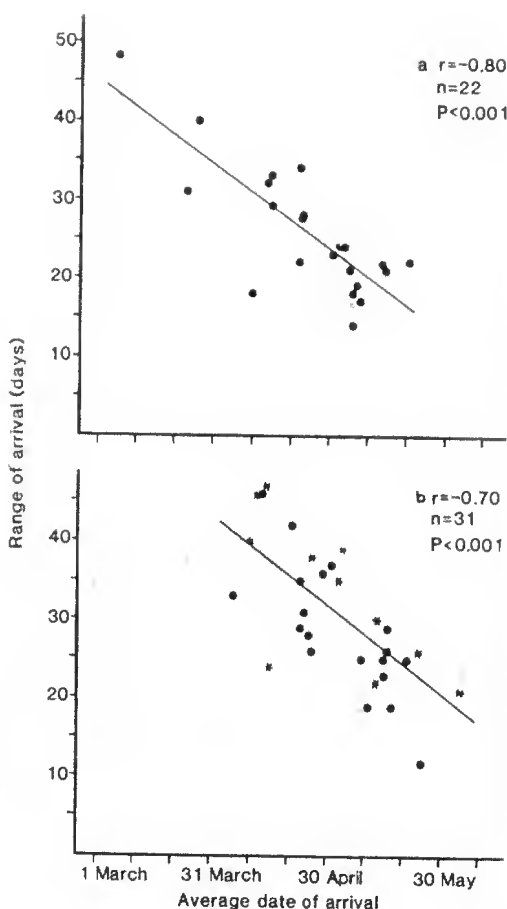
F i g. 4. Annual variation in the arrival dates (range) in relation to the mean date of arrival of the bird species at Oslo (a: 60°N) and Mosjöen (b: 66°N), respectively. Closed circles indicate values for passerine species (from Slagsvold, 1976b)

the time of the disappearance of local snow-cover (Högstedt, 1974; Slagsvold, 1977; Byrkjedal, 1980). For egg-laying and feeding its young some species depend on a supply of certain invertebrates, which must have reached a certain stage of development in spring before they are suitable as food items (e.g. Geometridae larvae), whereas others, to a greater extent, feeds on insects which have overwintered as imagos, or as larvae or pupae, and which therefore only require a onset of a few warm days before they become active adults.

That the arrival dates of migrants are not static is illustrated by data from Finland, viz. during the first half of the present century the mean recorded arrival dates of several passerines became more and more advanced. This was correlated with a progressive change to higher air temperatures in spring and a consequent earlier development of the vegetation (von Haartman, 1956; Berthold, 1971; Pikula, 1974; Williamson, 1975).

642

# HOW CAN A BIRD PREDICT WHEN BEST TO ARRIVE IN ITS BREEDING AREA

The early-arriving bird species typically winter close to their breeding areas, so close that they are subject to influence by the climatic conditions which prevail on their breeding grounds the following spring. Thus, by remaining in the same climatic region during the winter, they are able to time their return to the breeding grounds so soon as the environmental conditions there permit. The late-arriving species are typically long-distance migrants and have to rely on their internal circannual clocks to predict the best time of arrival.

Pikula (1971) found that the annual variation in the dates of the first records of the Song Thrush in spring in Czechoslovakia was lower at higher altitudes than at lower-lying localities. He presumed that the degree of variation in the climatic conditions of higher altitudes was probably less. A closer study of the predictability of the climate prevailing at different altitudes is therefore to be recommended.

Alerstam and Högstedt (1980) have suggested that the date of the annual onset of spring is more variable in temperate than in arctic regions. However, so far as the air temperature and habitat phenology in spring are concerned, this does not seem to hold true (Slagsvold, 1976a, in press; Irving, 1960; Myers, Pitelka, 1979). Indeed, at northern latitudes, the vegetation often develops very suddenly in spring, but the timing of this sudden leafing and flowering varied greatly from year to year, depending on the onset of the abrupt rise in air temperature induced by a shift from a northerly to a southerly air-flow. At Tana (70°N) in northern Norway, for instance, the annual range in the dates of birch leafing, even over a period of only three years, was as much as three weeks. It is thus virtually impossible for birds which winter in tropical areas to predict the environmental conditions which they will encounter when they return to their northern breeding areas.

As mentioned above, the annual variation in the arrival and breeding times of migrants is less at high than at low latitudes. It would thus appear that the time of the onset of spring is more predictable at high than at low latitudes, in the sense that the duration of the optimal period for arrival and breeding seems to be shorter. According to Alerstam and Högstedt (1980) this circumstance permits those birds which breed at high latitudes to winter far away and may thus provide an explanation for the phenomenon of "leap-frog migration".

I have studied the annual variation in the date on which a certain air temperature level is attained for the first time in spring, and also the annual variation in the daily air temperature on certain days in spring(Slagsvold, 1976a). I found that these annual variations were not of a lesser degree later on rather than early on in spring. However, even though the air temperatures in late spring also varied considerably, the mean temperature is nevertheless then higher and so the chances of such climatic disasters as catastrophic late snowfalls are reduced.

## WHY DOES SUCH A LOW CORRELATION EXIST BETWEEN THE ARRIVAL TIMES OF BIRDS AND THE STAGES OF HABITAT PHENOLOGY?

The spring migration of birds appears to be so timed that the birds arrive on their breeding grounds at almost the earliest possible moment at which they

have a reasonable chance of surviving there (Lack,1960). It therefore seems
reasonable to expect to find that the northerly displacement in the arrival
dates of the birds will parallel the annual and geographical displacement of
the onset of spring. However, this does not seem to be the case for all spe-
cies of birds, and why not? How do they manage to survive after such a  phe-
nologically speaking, early arrival in a "late" year and at higher latitudes,
despite the low temperatures and the retardation in vegetational development,
and how even to defend their territories, build their nests and lay eggs?
This is probably an adaptation to the delayed and short spring season in such
"late" years and in such "late" areas. But why then do they not also arrive
correspondingly earlier in their more southern breeding areas?

The northern populations depart from their winter quarters some time after
the more southern populations have already left. The former thus remain lon-
ger in areas subject to high air temperature and advanced vegetational deve-
lopment, and their winter quarter may be situated farther south as well. The
northern populations may therefore be in a better physiological condition at
the time of arrival on their breeding grounds even though they have to fly
further to reach them. Studies of body fat content may provide an answer to
the question whether the birds belonging to the more northern populations are
able to replenish their fat reserves on arrival or en route north (Slagsvold,
1976b). For instance, there may be relatively more food available the further
north one goes, when similar stages of vegetational development are compared,
because of longer days and of a lower diversity of the food items (von Haart-
man, 1973; Levin, Turner, 1977). This may be a food supply such as plant seeds
from the preceding year, which is not directly dependent upon air temperature
and the requisite vegetational and invertebrate development in spring. Arthro-
pods produced in the previous year may also be of great importance. As one
progresses northwards the life-cycle type of many insects changes, with con-
sequences in their appearance times and availability (Bradshaw, 1974). Weid-
emeyer (1973) has suggested that the annual variation in migrant arrival dates
should be less for bird species which rely mainly upon seeds left over from
previous seasons, or on aquatic foods, than for insectivorous species (Nisbet,
Drury, 1968; Sealy, 1975). However, over a 50-year observation period, he
found that in fact the reverse was true.

For each explanation provided for the early arrival of migrants in nort-
hern areas, the question must be answered: why is this not also the case for
bird populations breeding in the more southern, due to natural selection for
early arrival? In these areas, too, the birds return from wintering in warmer
areas, with a more advanced state of vegetational development, and they also
have a shorter distance to travel. Plant seeds and aquatic foods may also be
available there on arrival. Detailed feeding and food supply studies are the-
refore called for. The relatively early arrival and breeding of birds at high
latitudes seems in particular remarkable, because food supply constraints have
frequently been put forward as setting a limit to an early, otherwise favou-
rable, onset of breeding (Perrins, 1970; Jones, Ward, 1976; Drent, Daan,1980).
An early arrival of birds at high altitudes, phenologically speaking, is more
easily understandable from an energetic standpoint than an early arrival at
high latitudes, since the birds inhabiting mountain areas can rapidly retreat

to lower-lying localities if the weather subsequently turns bad. A possible explanation for the low degree of annual variation found in the arrival dates of "late-returning" species is that at this time of year enough food is generally available for survival, even if the weather subsequently turns bad (Salomonsen, 1967). However, further feeding and food supply studies are required and a further question requires an answer, viz. why don't these species, at least some individuals or flocks, arrive at a still earlier date if it is so favourable, ultimately, to settle early and start breeding early?

Consequently, the time of arrival and the onset of breeding of birds may not be as early in spring as the energy demand would allow. Other biotic factors, such as predation pressure and the degree of intraspecific competition are also important. For instance, the rate of nest predation is generally higher early on than later on in the breeding season, and is also higher at low than at high latitudes (Slagsvold, 1982). In other words, the selection pressure for an early onset of breeding may be relaxed in more southerly compared to more northerly areas (Byrkjedal, 1980). On the other hand, the competition for breeding territories is probably more severe at southern latitudes, and this will favour those birds which arrive early. Thus, whereas the main problems for birds which occupy breeding areas at low latitudes are nest predation and competition for territories, nest sites and mates, the important factors for those breeding at high latitudes are food availability and the length of time available for any successful breeding at all to take place.

In Norway the various migrant bird species arrive in about the same order each year, and also from place to place, forming separate temporal groups (e.g. species 7-15 in Fig. 5). A close relationship exists between arrival time, food availability and food requirements. Species which arrive early utilize the seeds which have been left over from the previous year, those arriving late are typically insectivores. However, there appear to be certain exceptions which call for further study. Studies of congeneric species in particular are to be recommended, e.g. the Chaffinch Fringilla coelebs and the Brambling F.montifringilla (Slagsvold, 1979; Mikkonen, 1981a,b), as well as the different Phylloscopus species. For instance, among those birds which are mainly insectivorous, the Chiffchaff P.collybita arrives relatively early on in spring in Norway, whereas the closely-related Willow Warbler P.trochilus arrives two or three weeks later (Fig. 5) but starts egg-laying only a few days later than does the Chiffchaff (Haftorn, 1971).

SUMMARY

The spring migration of birds appears to be so timed that the birds arrive on their breeding grounds at almost the earliest possible moment at which they have a reasonable chance of surviving there. It therefore seems reasonable to expect to find that the annual and geographical displacement in the arrival dates of the birds will parallel the annual and geographical displacement of the "onset of spring". For many species this does not seem to be the case, and this raises questions of proximate and ultimate character: how do the northern populations manage to survive and breed after such a, phenologically speaking, early arrival at high latitudes, and why do not the southern populations of birds arrive earlier, due to strong natural selection for early arrival and breeding? Probably, answers to the questions are found
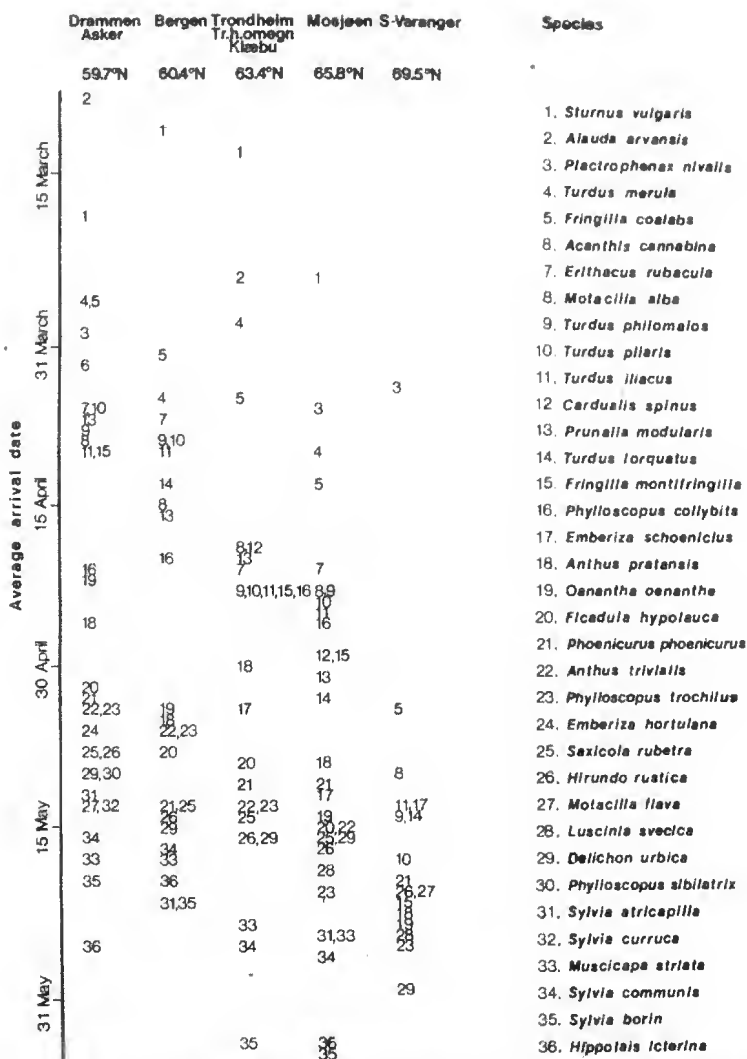
Fig. 5. The arrival dates of migrant passerine birds in Norway (data from Haftorn, 1971)

| | Drammen Asker 59.7°N | Bergen 60.4°N | Trondheim Tr.h.omegn Klæbu 63.4°N | Mosjøen 65.8°N | S-Varanger 69.5°N | Species |
|---|---|---|---|---|---|---|
| | 2 | | | | | 1. *Sturnus vulgaris* |
| 15 March | | 1 | | | | 2. *Alauda arvensis* |
| | | | 1 | | | 3. *Plectrophenax nivalis* |
| | 1 | | | | | 4. *Turdus merula* |
| | | | | | | 5. *Fringilla coelebs* |
| | | | | | | 6. *Acanthis cannabina* |
| | | | 2 | 1 | | 7. *Erithacus rubecula* |
| | 4,5 | | | | | 8. *Motacilla alba* |
| 31 March | 3 | | 4 | | | 9. *Turdus philomelos* |
| | | 5 | | | | 10. *Turdus pilaris* |
| | 6 | | | | 3 | 11. *Turdus iliacus* |
| | 7,10 | 4 | 5 | 3 | | 12. *Carduelis spinus* |
| | 8,13 | 7 | | | | 13. *Prunella modularis* |
| | 11,15 | 9,10 / 11 | | 4 | | 14. *Turdus torquatus* |
| 15 April | | 14 | | 5 | | 15. *Fringilla montifringilla* |
| | | 8 / 13 | | | | 16. *Phylloscopus collybita* |
| | | | 8,12 / 13 | | | 17. *Emberiza schoeniclus* |
| | 16 | 16 | 7 | 7 | | 18. *Anthus pratensis* |
| | 19 | | 9,10,11,15,16 | 8,9 / 10 / 16 | | 19. *Oenanthe oenanthe* |
| | 18 | | | | | 20. *Ficedula hypoleuca* |
| 30 April | | | 18 | 12,15 / 13 | | 21. *Phoenicurus phoenicurus* |
| | 20 / 21 | | 17 | 14 | | 22. *Anthus trivialis* |
| | 22,23 | 19 / 18 | | | 5 | 23. *Phylloscopus trochilus* |
| | 24 | 22,23 | | | | 24. *Emberiza hortulana* |
| | 25,26 | 20 | 20 | 18 | 8 | 25. *Saxicola rubetra* |
| | 29,30 | | 21 | 21 / 17 | | 26. *Hirundo rustica* |
| 15 May | 31 / 27,32 | 21,25 / 28 / 29 | 22,23 / 25 / 26,29 | 19,22 / 28,29 / 28 | 11,17 / 9,14 | 27. *Motacilla flava* |
| | 34 | 34 / 33 | | | 10 | 28. *Luscinia svecica* |
| | 33 | 36 | | 23 | 21,26,27 | 29. *Delichon urbica* |
| | 35 | 31,35 | 33 | 31,33 | | 30. *Phylloscopus sibilatrix* |
| | 36 | | 34 | 34 | 29 | 31. *Sylvia atricapilla* |
| 31 May | | | | | | 32. *Sylvia curruca* |
| | | | 35 | 36,35 | | 33. *Muscicapa striata* |
| | | | | | | 34. *Sylvia communis* |
| | | | | | | 35. *Sylvia borin* |
| | | | | | | 36. *Hippolais icterina* |

Average arrival date

in the differences in basic conditions for reproduction: whereas the main problems for birds which occupy breeding areas at low latitudes are nest predation and competition for territories, nest sites and mates, the important factors for those breeding at high latitudes are food availability and the length of time available for any successful breeding at all to take place.

References

Alerstam T., Högstedt G. – Ornis Scand., 1980, 11, p. 196–200.

Baker J.R. – In: Evolution: essays on aspects of evolutionary biology / Ed. by G.R. de Beer. Oxford, Univ. Press, London; New York, 1938, p. 161–177.

Berthold P. – In: Grundriss der Vogelzugskunde / Ed. by E.Schüz. Parey, Berlin und Hamburg, 1971, p. 257–299.

Bradshaw W.E. – In: Phenology and seasonality modeling (Ecological Studies 8)/ Ed. by H.Lieth. Berlin; Heidelberg; NY : Springer-Verlag, 1974, p. 127–137.

Byrkjedal I. - Ornis Scand., 1980, 11, p. 249-252.

Danilevskii A.S. Photoperiodism and seasonal development of insects. Edinburgh; London: Oliver and Boyd, 1965.

Drent R.H., Daan S. - Ardea, 1980, 68, p. 225-252.

Haartman L. von. - Soc. Scient. Fenn. Årsbok, 1956, 33B, p. 1-23.

Haartman L. von. -Ornis Fenn., 1968, 45, p. 1-7.

Haartman L. von. - In: Breeding biology of birds / Ed. by D.S.Farner. Natl. Acad. Sci., Wash., D.C., 1973, p. 435-437.

Haftorn S. Norges Fugler. Oslo: Universitetsforlaget, 1971.

Hemmingsen A.M. -Proc. Int. orn. Congr., 1951, 10, p. 289-294.

Hopkins A.D. - U.S. Dept. Agr. Misc. Publ., 1938, 280, p. 1-188.

Hussell D.J.T. - Ecol. Monogr., 1972, 42, p. 317-364.

Högstedt G. -Ornis Scand., 1974, 5, p. 1-4.

Immelmann K. - In: Avian Biology / Eds. D.S.Farner, J.R.King. N.Y.: Academic Press, 1971, p. 341-389.

Irving L. - U.S. Natl. Mus., Bull., 1960, 217, p. 1-409.

Jones P.J., Ward P. - Ibis, 1976, 118, p. 547-574.

Lack D. - Auk, 1960, 77, p. 171-209.

Lack D. - Oikos, 1968, 19, p. 1-9.

Levin D.A., Turner B.L. - In: Evolutionary ecology / Eds. B.Stonehouse, C.Perrins. L.: Macmillan Press, 1977, p. 215-222.

Lieth H. - In: Phenology and seasonality modeling (Ecological studies 8)/ Ed. by H.Lieth. Berlin; Heidelberg; New York: Springer-Verlag, 1974, p.3-19.

Maclean S.F. Jr., Pitelka F.A. - Arctic, 1971, 24, p. 19-40.

Mikkonen A. - Ornis Fenn., 1981a, 58, p. 78-82.

Mikkonen A. - Ornis Scand., 1981b, 12,p. 194-206.

Myers J.P., Pitelka F.A. - Arct. Alp. Res., 1979, 11, p. 131-144.

Nisbet I.C.T., Drury W.H. Jr. - Anim. Behav., 1968, 16, p. 496-530.

Ojanen M. - Ornis Fenn., 1979, 56, p. 148-155.

Perrins C.M. - Ibis, 1970, 112, p. 242-255.

Pikula J. - Zool. Listy, 1971, 21, p. 165-180.

Pikula J. - Zool. Listy, 1974, 23, p. 163-174.

Pikula J. - Zool. Listy, 1976, 25, p. 65-72.

Salomonsen F. Fugletraekket og dets Gåder. København: Munksgaard, 1967.

Schüz E. Grundriss der Vogelzugskunde. Parey, Berlin; Hamburg, 1971.

Sealy S.G. - Auk, 1975, 92, p. 528-538.

Siivonen L. - Suomal. elain - ja kasvit. Seur. van. elain. Julk., 1939, 7, p. 1-289.

Silverin B. - Ornis Scand., 1981, 12, p. 133-139.

Slagsvold T. - Norw. J. Zool., 1975, 23, p. 213-218.

Slagsvold T. - Ornis Scand., 1976a, 7, p. 127-145.

Slagsvold T. - Norw. J. Zool., 1976b, 24, p. 161-173.

Slagsvold T. - Ornis Scand., 1977, 8, p. 197-222.

Sokolov L.V. - Zool. Zh., 1975, 54, p. 257-265.

Stresemann E. - Vår Fågelvärld, 1948, 7, p. 1-18.

Väisänen R.A. - Ornis Fenn., 1974, 51, p. 61-84.

Wallentinus H.-G. - Vår Fågelvärld, 1970, 29, p.160-178.

Weydemeyer W. - Condor, 1973, 75, p. 400-413.

Williamson K. - Bird Study, 1975, 22, p. 143-164.

SOCIAL BEHAVIOR AND FORAGING ECOLOGY OF
NEOTROPICAL MIGRANTS

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INTRODUCTION

Migrant birds often move between havitats that are dramatically different
in structure and food resources. They must function efficiently to raise
young in food rich breeding habitat , as well as survive possible food shor-
tages in winter habitats. How birds are adapted for the seasonal occupation
of different habitats can best be approached by examining the foraging be-
havior, social behavior,and morphology of individual species. The large num-
ber of migrant species, each with its unique combination of winter and breed-
ing distributions and food habits, provides a rich pool to explore for cross-
seasonal correlations.

I have selected neotropical migrant passerines as the focus of a review of
the social organization and feeding eoology of species on their wintering
grounds. I will focus on the relationship of sociality and foraging and how
these relate to other aspects of species' biology.

SOCIAL ORGANIZATION

Eaton (1953) first noted the consistent difference in social behavior of
different species of migrant parulids in Cuba.Since his initial observations,
many other observers have noted the species-specific diversity of winter so-
cial organization in neotropical migrant birds (Skutch, 1957; Willis, 1966;
Lack, Lack, 1972; Rappole, Warner, 1980; Greenberg, 1979, in press; Hespen-
heide, 1980; Morton, 1980; Tramer, Kemp, 1980).

Most neotropical migrant species characteristically occur solitarily;  the
occurrence of single species flocks is a relatively uncommon phenomena found
commonly in about a dozen species (Table 1). The intraspecifically gregarious
migrants span the taxonomic categories including Tyrannidae, Vireonidae, Tur-
didae, Parulidae, Icteridae, and Fringillidae. For most of these species
flock size is small ( < 20 individuals), but some groups may be huge, such as
those found in Tyrannus tyrannus (Morton, 1972).

The most intriguing social grouping for migrant birds is the non-breeding
male/female pair (Table 1). The occurrence of pairs of neotropical migrants
was discovered recently (Leck, 1872; Morton, 1980; Greenberg, Gradwohl,1980),
although winter pairs are well known for certain partial migrants in the tem-
perate zone (Lack, 1943; Zahavi, 1971; Davies, 1977). The mechanism of pair
formation is not known and the handful of species that are known to occur in
winter pairs remains too disparate to support a simple adaptive hypothesis.

Formerly, the occurrence of territorial defense was a noteworthy event
(Schwartz, 1967; Emlen, 1973), but it is now viewed as a dominant theme in
the life of neotropical migrants (Rappole, Warner, 1980; Morton, 1980). Ter-
ritoriality, however, is a rubric that covers at least two distinct phenomena
in wintering migrants: the long-term defense of a patch of habitat through an
entire winter; and the short-term defense of a specific resource.

T a b l e   1. Winter social behavior of some neotropical migrant passerines

|  | Single species flocking |
|---|---|
| Tyrannus tyrannus | Morton, 1972; Fitzpatrick, 1980; Leck, 1968 |
| Hylocichla ustalata | Willis, 1966; Rappole and Warner, 1980; |
| Vireo olivaceus | Morton, 1980 |
| Vermivora peregrina | Griscom, 1932; Skutch, 1957; Tramer and Kemp, 1979; Morton, 1980 |
| Vermivora ruficapilla | pers. obs. |
| Protonotarea citria | Morton, 1980 |
| Dendroica coronata | MacArthur, 1958; Wilz and Giampa, 1978 |
| Dendroica palmarum | Eaton, 1953 |
| Dendroica tigrina | pers. obs. |
| Dendroica castanea | Greenberg, 1979; in press |
| Dendroica striata | DeSchauensee and Phelps, 1978 |
| Icterus spurius | Hamilton, 1961; Morton, 1979; Rappole and Warner, 1980 |
| Pheucticus ludovicianus | Rappole and Warner, 1980 |
| Passerina cyanea | Rappole and Warner, 1980 |

|  | Pairs |
|---|---|
| Protonotarea citrea | Morton, 1980 |
| Dendroica cerulea | pers. obs. |
| Wilsonia canadensis | Greenberg and Gradwohl, 1980 |
| Piranga rubra | Leck, 1972 |
| Icterus galbula | Leck, 1972 |
| Vireo solitarius | Morton, pers. comm. |
| Vireo phildelphicus ? | Tramer and Kemp, 1980 |

Can occur in flocks

Long-term territoriality will probably be found to be a dominant social system of migrant birds when many more studies of color-marked individuals are completed (Rappole, Warner, 1980; Greenberg, in press). Short-term defense has attracted considerable attention in the "notes" section of ornithological journals. Species that otherwise are not territorial, and in fact are often intraspecifically gregarious, often display short-term defense. Consider that the phenomena has been reported in the following species also listed in Table 1: Vermivora peregrina (Morton, 1980; Tramer, Kemp, 1979), Dendroica tigrina (Kale, 1967; pers. obs.), D.coronata (Woolfenden, 1962), D.castanea (Morton, 1980), D.palmarum (Wunderle, 1978), Icterus galbula (Schemske, 1975; Cruden, Hermann-Parker, 1977).

FORAGINIG BEHAVIOR

Most species of migrant birds that breed in forests and woodlands search for insects that rest on foliage (Holmes et al., 1979). A smaller number of species forage in the leaf litter for soil arthropods (Turdidae) or sally to caputra aerial insects (Tyrannidae); one species searches the bark of trees for insects (Mniotilta).

During the non-breeding season, most migrants remain foliage insectivores,

T a b l e  2. Omnivorous species of neotropical migrant passerines

| | |
|---|---|
| Tyrannus tyrranus | Morton, 1973; Fitzpatrick, 1980; Willis, 1966; Rappole and Warner, 1980; Morton, 1980 |
| Hylocichlus ustulata | Willis, 1966; Leck, 1968 |
| Vireo olivaceus | Morton, 1980 |
| Vermivora peregrina | Griscom, 1932; Skutch, 1957; Tramer and Kemp, 1979; Greenberg, 1980; Morton, 1980 |
| Vermivora ruficapilla | pers. obs. |
| Protonotaria citria | Morton, 1980 |
| Dendroica coronata | MacArthur, 1958; Wilz and Giampa, 1978 |
| Dendroica palmarum | |
| Dendroica tigrina | pers. obs. |
| Dendroica castanea | Morton, 1980; Greenberg, 1979; in press |
| Piranga rubra | Leck,1972 |
| Piranga olivacea | pers. obs. |
| Icterus spurius | Morton, 1980 |
| Icterus galbula | Schemske, 1975; Crudend and Hermann-Parker, 1977; Leck, 1974 |
| Pheucticus ludovicianus | Morton, pers. comm. |
| Passerina cyanea | Rappole and Warner, 1980 |

but  both inter- and intraspecific variation in niche increases. In some
birds this increased variation involves shifts in what microhabitats are
searched, and in other species this consists of feeding on new kinds of food,
particularly fruit and nectar.

Migrant birds can be placed into three categories based on their use of
fruit or nectar: restricted insectivores (0% omnivory); partial omnivores
(0-10%); omnivores ( >10%). Most species remain mostly  or wholly insecti-
vorous and the known omnivorous species are listed in Table 2.

Whereas behavioral plasticity has been considered the hallmark of migrant
bird behavior (Morse, 1971; Willis, 1966), it may be a rather rare strategy
of migrant birds to be extremely generalized.  If attention is paid to the
foraging ecology of birds in one community (such as in Rappole, Warner, 1980;
Willis, 1966; Tramer, Kemp, 1980; Lack, Lack, 1972; Greenberg, in press),
migrant birds show a degree of specialization comparable to resident birds.
A few species of migrants stand out as being extremely generalized in where
they search for food. No species displays this plasticity more conspicuously
than Dendroica coronata which forages in a broad range of habitats and sub-
strates. On the other extreme, a few species of migrant birds regularly spe-
cialize on certain typically tropical microhabitats. Helmitheros  vermivora
and Vermivora chrysoptera in lowland tropical forest forage out of dead cur-
led leaves that hang in the forest understory. In highlands, V.chrysoptera
specialize upon foraging from epiphytes (Powell, 1980; pers. obs.). These
species may forage out of dead curled leaves in the Temperate Zone to a
lesser degree.

## THE RELATIONSHIP OF FORAGING BEHAVIOR AND SOCIAL BEHAVIOR

The diversity of social systems of wintering migrant birds reflects a diversity of foraging strategies. The correlation is similar to the one found by Crook (1965) for Ploceidae. The species that occur in single species flocks are those species that are most omnivorous ($X^2 = 31.5$, d.f. = 2, $p < .001$). While these omnivorous species occur in flocks, they often aggressively defend certain fruiting and flowering trees. These species are best characterized as having labile social organization (Tramer, Kemp, 1979).

The dichotomy in social organization of omnivorous versus more insectivorous migrants is probably related to the defensibility of home-range sufficiently large to contain a winter's food supply. The patchy and ephemeral nature of fruiting and flowering trees probably requires an animal to range over a large area to use these resources throughout the winter. It may require birds to move large distances. Insectivorous migrants can presumably survive the winter on a particularly good patch of habitat provided that conspecific interlopers are excluded. Single species flocking is a possible, but not necessary consequence of the large overlapping home ranges of the omnivorous species. The important point is that the omnivorous species, freed from a commitment to a long-term territory, can show greater lability in social organization.

### CORRELATES OF WINTER DIET

The most profound and readily identifiable ecological division among wintering migrants is their degree of omnivory. Finding features of the biology of migrant species that allow us to predict how omnivorous it will be on the wintering grounds should prove of particular interest. The following generalizations can be advanced:

Size: Larger species of migrants have a much greater chance of being omnivorous than smaller species. Of the migrant species over 15 grams (for which some data are available) 11 of 17 are omnivorous of migrants weighing 15 grams or less, eight of 40 are omnivorous ($X^2 = 4.8$, d.f. = 1, $p < .05$).

Phylogenetic Relationships: Certain taxonomic classes of migrants consist of restricted insectivores. Within Parulidae, for example, most of the genera (Wilsonia, Orporornis, Sciurus, Mnioltilta, Helmitheros, Setophaga) contain species that probably never take plant products. Dendroica and Vermivora have numerous species that at least occasionally eat fruit and nectar.

While a dependence upon plant foods may require a large shift in winter social behavior, the low-level use of fruit often occurs in basically insectivorous species of tropical birds. A complete restriction to insectivory may be based on some rigid psychologically-based restraints.

Breeding Habitat: Within Dendroica and Vermivora most of the omnivorous species are restricted boreal forest breeders (V.peregrina, D.tigrina, D.castanea, D.coronata and D.palmarum); three of these species are major budworm species (Kendeigh, 1945).

These patterns suggest that a highly omnivorous diet is selected by species unable to persist as strict insectivores during the non-breeding season:
a) Large species should be less likely to subsist on insects because large

active tropical arthropods are probably disproportionately more difficult for less specialized insectivores to capture.

b) Birds restricted to boreal forest, and particularly those species that depend heavily upon superabundant budworms, are probably species less able to efficiently glean insects from broad-leafed foliage during the non-breeding season (Greenberg, 1979)

CONCLUDING REMARKS

As homogeneous as most temperate forest passerines are during the breeding season, both ecologically and socially, they show great variation during the non-breeding season. However, the divergent winter behavior of some species, such as the waxwing-like flocks of Tyrannus, and "beach-combing" of Dendroica coronata, belie the more typically conservative behavior of most neotropical migrant passerines. Most species remain insectivorous, exploiting microhabitats similar to those used in the breeding season. Many species defend small territories throughout the winter.

Perhaps the driving force behind the increased variation in foraging behavior in the winter months is the break-down of the monogamous territorial social system (in most species) and the increase of alternative food sources during the winter months, particularly in tropical areas.

The omnivory-insectivory dichotomy is fundamental to the diversification of winter ecology of migrant species. Why some temperate zone insectivores remain insectivorous, while others become more omnivorous is a critical question to answer both in an ultimate and proximate sense. Since most small fruit are relatively easily procurred, omnivory may allow some successful temperate-breeding insectivores to winter in areas where they are unable to subsist on insects.

R e f e r e n c e s

Bond J. - In: The Warblers of North America / Eds. L.Griscom, A.Sprunt.
    N.Y.: Devin-Adair, 1957, p. 257-263.
Crook J. - Symp. Zool. Soc. London, 1965, p. 181-218.
Crudend R.W., Hermann-Parker S.M. - Auk, 1977, 94, p. 594-596.
Davies N.B. - J. Anim. Ecol., 1977, 46, p. 37-57.
Deschauensee R., Phelps W. A guide to the Birds of Venezuela. Princeton,
    N.J. Princeton Univ. Press, 1978.
Eaton S.W. - Wilson Bull., 1953, 65, p. 169-174.
Emlen J.T. - Wilson Bull., 1973, 85, p. 71-74.
Fitzpatrick J. -In: Migrant Birds in the Neotropics: Ecology, Behavior,
    Distribution and Conservation / Eds. A.Keast, E.Morton. Wash., D.C.,
    Smithsonian Press, 1980, p. 67-78.

Greenberg R., Gradwohl J. - Ibis, 1980, 122, p. 509-512.

Greenberg R. - Auk, 1979, 96, p. 756-766.

Greenberg R. - Biotropica, 1981, 13, p. 215-223.

Griscom L. - Bull. Amer. Mus. Nat. Hist., 1932, 64, p. 3-24.

Hamilton T. - Am. Nat., 1961, 95, p. 121-124.

Hespenheide H. - In: Migrant Birds in the Neotropics: Ecology, Behavior,
    Distribution and Conservation / Eds. A.Keast, E.Morton. Wash., D.C.,
    Smithsonian Press, 1980, p. 227-239.

Holmes R.T., Bonney R.E., Pacala S.W. - Ecology, 1979, 60, p. 512-520.

Kale H. - Auk, 1967, 84, p. 120-121.

Kendeigh C.S. - Auk, 1945, 62, p. 418-436.

Lack D. The Life of the Robin. L.: H.F. and G.Witherby, 1943.

Lack D., Lack J. - Living Bird, 1972, 11, p. 87-95.

Leck C.F. - Bird Banding, 1968, 39, p. 318.

Leck C.F. - Auk, 1972, 89, p. 842-850.

Leck C.F. - Auk, 1974, 91, p. 162-163.

Macarthur R. - Ecology, 1958, 39, p. 599-619.

Morse D. - Annual Review of Ecology and Systematics, 1971, 2, p. 177-200.

Morton E. - Auk, 1971, 88, p. 925-926.

Morton E. - Ann. Miss. Bot. Garden, 1979, 66, p. 482-489.

Morton E. - In: Migrant Birds in the Neotropics: Ecology, Behavior, Distri-
    bution and Conservation / Eds. A.Keast, E.Morton. Wash., D.C., Smithso-
    nian Press, 1980, p. 437-466.

Powell G. - In: Migrant Birds in the Neotropics: Ecology, Behavior, Distri-
    bution and Conservation / Eds. A.Keast, E.Morton. Wash., D.C., Smithsonian
    Press, 1980, p. 477-485.

Rappole J., Warner D. - In: Migrant Birds in the Neotropics: Ecology, Behav-
    ior, Distribution, and Conservation / Eds. A.Keast, E.Morton. Wash., D.C.,
    Smithsonian Press, 1980, p. 353-395.

Schemske D. - Auk, 1975, 92, p. 594-595.

Schwartz P. - Living Bird, 1964, 3, p. 169-184.

Skutch A. - In: The Warblers of North America / Eds. L.Griscom, A.Sprunt.
    N.Y.: Devin-Adair, 1957, p. 275-286.

Timken R.L. - Wilson Bull., 1970, 82, p. 184-188.

Tramer E., Kemp T. - Auk, 1979, 96, p. 186-187.

Tramer E., Kemp T. - In: Migrant Birds in the Neotropics: Ecology, Behavior,
    Distribution, and Conservation / Eds. A.Keast, E.Morton. Wash., D.C.,
    Smithsonian Press, 1980, p. 285-296.

Willis F. - Living Bird, 1966, 5, p. 187-231.

Wilz K., Giampa V. - Wilson Bull., 1978, 90, p. 566-574.

Woolfenden G. - Auk, 1962, 79, p.713-714.

Wunderle J. - Wilson Bull., 1978, 90, p. 297-299.

Zahavi A. - Ibis, 1971, 113, p. 203-212.

THE ROLE OF HEREDITY AND OF COLLECTIVE AND INDIVIDUAL
EXPERIENCES IN SEASONAL DISTRIBUTION AND MIGRATION OF BIRDS

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Every bird species can be regarded as a complex population system charac-
terized by relatively stable links with the areas they populate, these links
being consolidated not only eco-morphologically, but also via inherent col-
lective stereotypes of behaviour, as well as collective and individual ex-
perience.

The most essential feature of large geographical populations of avian
species is a common major direction of seasonal migrations. This feature is
one of the elements of the species behaviour stereotype as has been proved
by a number of well-designed experiments on avian orientation. The inherent
directions of avian migrations are invaraibly justified biologically as the
most rational routes from nesting to wintering sites. These routes are pre-
sented diagrammatically in Fig. 1. Examples of large geographical populations
of birds in the USSR are provided by: Atlantic populations, migrating west-
ward and southwestward; populations migrating southward, i.e. to the Near
East and India; those migrating south-eastward, i.e. to China and Japan and
others. Many of the above-mentioned gross populations may be further speci-
fied and divided into several minor populations. For several duck species
such a study was performed by T.P.Shevareva (1968, 1970), and for a number
of other birds - by A.A.Kistchinsky (1978, 1979). It should be noted that
the natural conditions of the nesting areas of birds pertaining to a single
geographical population may differ considerably.

The next hierarchical grade in the species population structure is re-
gional geographical populations. Their common feature is similarity of eco-
logical conditions in the breeding areas. At the same time, the major routes
of seasonal migrations, and partially, their major trends may differ within
the nesting area occupied by the same population depending on the ecological
conditions favourable for migration. Examples of regional geographical po-
pulations are furnished by some waterfowl species of the Pre-Caspian Lowland,
lake forest-steppe of the Trans-Urals, Western Siberia, Northern Kazakhstan,
etc. Each of them is largely independent. Their common feature is primarily
their individual behaviour stereotype adapted to the particular conditions
of respective breeding areas.

In addition to the above-mentioned categories, local populations should
be mentioned. They emerge in localities favourable for a particular species
and are normally isolated and separated from one another by localities that
are less favourable ecologically. Such are large tracts of well-preserved
mature forests among young stands, steppe plots among ploughed up land,
isolated lakes, built-up areas and their neighbourhood,, sea bays. The popu-
lations of such localities are consolidated through the so-called phylopat-
ry, i.e. development of common behavioural responses, which are rigidly
adapted to the life in a particular area. Such populations are maintained
through a merge of several such groups into a common flock or several
flocks, and also through following seasonal migration routes determined by
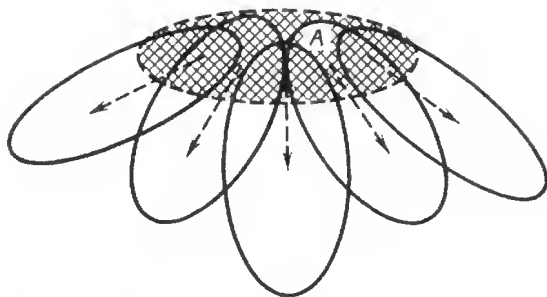
F i g. 1. Division of species range into distribution regions of major geo-
graphical populations. The nesting zone is cross-hatched, while zones of
migration and wintering are clear. Arrows show major directions of seasonal
migrations characteristic of large geographical populations

similar ecological conditions. Thanks to that, the experience acquired by
individual population members is passed on to the population as collective
experience.

The sharper the contrast between the areas occupied by local populations
and surrounding landscapes, the more independent such populations. The most
vivid examples are provided by nesting colonies of the Rook, Heron, Swift
and other species, as well as by local populations which also develop in
birds nesting singly. One of the factors promoting the formation of such po-
pulations is spring songs of males. They not only communicate that the ter-
ritory has been taken up by a nesting couple, but also that the given area
is favourable for nesting. According to N.B.Birulya (1960) these acoustic
cues are conducive to the regularity of nesting couples dispersal in nu-
merous species throughout the area suitable for nesting.

Of interest are also some particular sites that are regularly used by
individual couples or small groups as nesting ranges and places for feeding
and rest on migration routes or in wintering areas. These sites are charac-
terized by a set of ecological conditions which are favourable for the given
species. Many such sites are used by birds for many years running. As an il-
lustration, in 1949, V.V.Nemtzev found and mapped in the Darwin Reserve, 16
nesting ranges of the Crow, which were located within 7 kilometres from the
Reserve's research station. They all were located on the; edge of a forest,
commonly on the banks of a reservoir. In 1982, 15 nesting couples of the
Crow were recorded there, out of which number 10 had been stationed at the
same sites used for nesting as early as 24 years ago. Another 3 nesting
ranges showed some displacement of nests (by 200-300 m) due to various rea-
sons, and another 2 nests appeared at new sites over that period where clus-
ters of birches had grown among the meadow, and only 3 nesting ranges were
abandoned because they had been overgrown by a thick forest (Fig. 2). It is
noteworthy that in 1951-1954, in an experiment the Crow population was eli-
minated almost completely, the birds having been shot near the nests. The
experiment resulted in the number of nesting couples being reduced to 4.
Thus, it was new bird couples that populated the temporarily vacant nesting
ranges. It can be inferred from the above that: (1) nesting ranges have
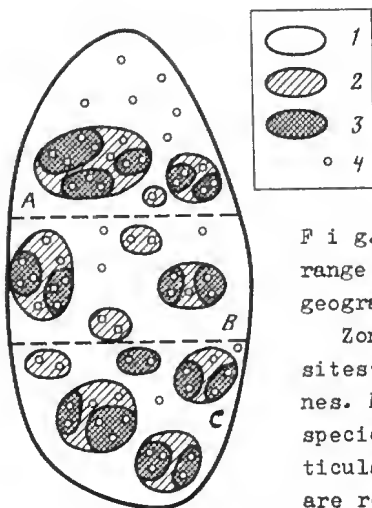
F i g. 2. A diagrammatic representation of species range landscape structure of that of its large geographical population

Zones of seasonal location of species: A— nesting sites; B— wintering sites, C— seasonal migration zones. Regions and areas varying in favourableness for species: 1— unfavourable, 2— favourable, 3— particularly favourable, 4— particular points which are regularly used by species and densely populated

some natural properties that distinguish them from the surrounding terrain and that the birds leave behind some traces of their occupancy, primarily, old nests which communicate to new residents that the range is favourable for nesting.

Bird wintering areas dating many years back are well known. These are primarily roosting sites. In Moscow, multi-thousand Crow and Jackdaw flocks have had a roosting site in the centre of the city in the park near the Kremlin walls for over one hundred years. In the Kyzyl-Agach Reserve on the Sara island a roosting site for a numerous wintering Milans and some other birds of prey located in a small smooth-leaved elm grove dates back to 60 years ago. In the same area in dense thickets of wild pomegranate trees and blackberry, the roosting site of a large association of Long-Eared Owls was found in 1930. V.V.Nemtzev and myself saw Owls at the same site after 28 years. Without giving further example I shall point out that such favourable concentrations of birds exist along every route of seasonal migrations.

In fact, Starlings spend the night in a definite area of reed thickets, while migratory Swifts bed in the growns of old willows, while migratory spotted Woodpeckers use the same feeding trees, etc. The same feature of bird behaviour is utilized in hunting migratory Geese from permanent huts set up on their route. Such constancy in visiting and use of the same sites by birds is of great significance in maintaining the unity of elementary and local populations. This unity is maintained via traces of past activity left behind at every such site. The permanence of response to these cues is provided through collective experience being passed over from generation to generation.

The peculiarities of ecological conditions of particular sites regularly used by birds are often hard to detect, but occasionally these can be determined and verified experimentally. A study of this type was performed by ornithologists of the Darwin Reserve. All the bird nests found there were described in a definite pattern to characterize: general features of

the biotope where nesting birds were recorded (forest and its type, meadow, bog, etc.); the particular small site where the nest was found, stating in a detailed manner its features, if only minor, to distinguish it from the surrounding sites; location and structure of the nest (e.g. a cluster of taller grass, a juniper shrub, a tree with a dense crown on forest edge, etc.). A large amount of data accumulated over a number of years were statistically treated, using a number of indices, which made it possible to develop a model for the nesting range in several bird species, reflecting, among other things, the peculiarities of nest location.

The next stage was an experimental verification of such models via construction of aritificial nesting ranges and attracting nesting couple. The experiments proved successful for Anas platyrhynchos, Anas penelope, Larus canus, Sterna hirundo, Haematopus ostralegus, Sylvia curruca, Sylvia communis and Ardea cinerea. I shall only mention 2 experiments that lend themselves to some general inferences. To establish a Heron colony, a cluster of artificial nests were constructed in tall pines on an island within several hundred metres from the laboratory. None of them were occupied by Herons which built their own nests near the man-made ones, the latter being used for construction material. The experiment has clearly demonstrated the cue significance of the experimental site. To attract the Common Gull (and also Duck and Snipel) for nesting, a portion of one of the islands was cleared of young pines and tall willow bushes, the turf was disturbed with a rake, and patches of sand soil cleared. The Gull colony formed at the site had 42 nests after 8 years. It existed for 25 years despite the fact that over those years both dense shrubs and trees were restored so that the site became quite unfavourable for Gulls. The colony had been maintained by force of "tradition" upheld by the population's collective experience.

Our concept of the hierarchical structure of an avian population and its territorial relationships with the range structure are represented diagrammatically in Table 1. Concurrently, a graphical illustration is provided in Fig. 2, which represents the physiographical structure of a species range of its large geographical populations. The Figure shows one of the possible combinations of regions and areas favourable for given species in definite seasons. The diagram in Fig. 3 shows a possible form of combination of various areas particularly favourable for the species in terms of their ecological conditions with ranges of regional and geographical populations. The mechanisms determining the boundaries of such ranges are shown diagrammatically in Fig. 4.

Another series of diagrams demonstrates consequitive changes of the ranges of regional populations due to the modification of the area by man. Felling, complete ploughing up of steppes and other forms of transformation of natural landscapes reduce areas particularly favourable for the species in different seasons (Fig. 5, 6). In a number of cases, the advent of anthropogenic landscapes (large waterbodies, forest plantations in steppe, etc.) promote deviation of migration routes and displacement of wintering sites (Fig. 7). But occasionally a situation arises when the distances between favourable areas become so great that migratory flocks are unable to cover them. In such cases, the ecological conditions peculiar to the route are disturbed
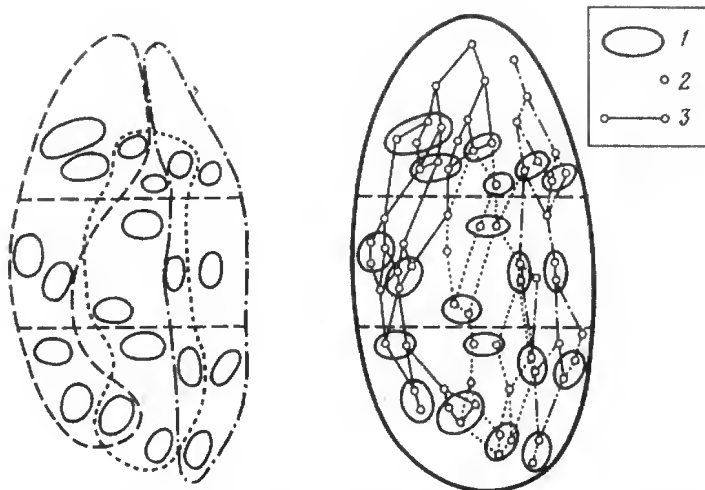
F i g. 3: Interrelationship of regions with ecological conditions particular-
ly favourable for species and ranges of associated geographical populations;
dashed line designates ranges of regional population, solid line - regions
with particularly favourable conditions

F i g. 4. Routes of seasonal migration between neighbouring points of con-
centrations of migrating individuals, as a basis for the development of
ranges of regional geographical populations

1 - regions particularly favourable ecologically;  2 - points of concent-
rations of migrating birds;  3 - migration routes between points of concent-
rations
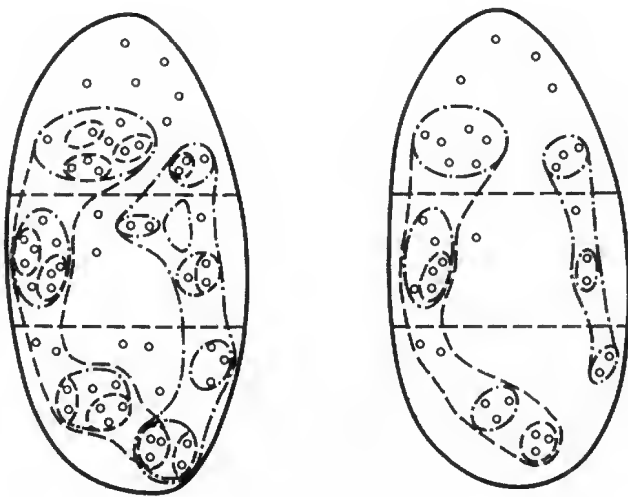


F i g. 5. Reduction in the number and area of regions particularly favoura-
ble for birds due to modification of the landscape by man. Disappearance
of some routes. Designations as in Fig. 3

F i g. 6. Further reduction in regions favourable for migrating birds and
emergence of fully-isolated populations. Designation as in Fig. 3

T a b l e  1. Hierarchical and spatial structure of species and range in birds

| Population structure of species | Range structure | |
|---|---|---|
| | Population | Landscape-geographical |
| Entire population of species | Entire area populated by Species Portions of range populated by species in different years, seasons and stages of biological cycle | Range whose borders are determined by physiographical (climatic and landscape) boundaries Parts of range with different ecological, primarily, climatio oonditions |
| Large geographical populations of species | Portions of range populations having considerable independence, characterized by definite nesting and wintering ranges, and also major directions of seasonal migrations | Areas, occasionally similar with respect to landscape. Often, they are separated by physiographical obstacles repesenting landscapes alien to species. Each of them has characteristic ecological conditions determining seasonal migration routes |
| Regional geographical populations | Regions populated by species at a greater density than adjoining areas. The populations are less isolated geographically than large geographical ones | Regions whose landscapes are much more favourable for species than adjoining areas |
| Local populations | Regions with populations having common behavioural features adjusted to local conditions and maintained thanks to flocking | Regions particularly favourable for species in different seasons due to their ecological conditions |
| Elementary, occasionally, seasonal communities | Sites regularly populated by individual couples or small groups of a given species thanks to a system of visual and audial cues created by birds themselves | Particular sites attractive for nesting, wintering or resting route |

to such a great extent that this endengers the existence of particular geographical populations. The only feasible solution is establishment of man-made sites favourable for species concerned along migration routes and in wintering areas (Fig. 8).
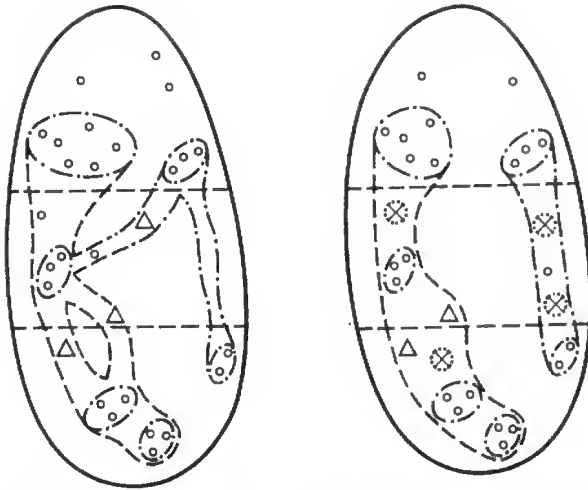
F i g. 7. Deviation of migration routes as a result of disappearance of natural biotopes and emergence of thropogenic areas used by species (triangle - favourable anthropogenic biotopes)

Triangles-anthropogenic areas, other designations as in Fig. 3

F i g. 8. Situation when it is necessary to create artificial sites along migration routes and in wintering areas for preserving regional populations of species. Cross, regions where such sites are to be created

The following inferences can be made. The major directions of seasonal migrations of large geographical populations are very stable and can hardly be apprecibly modified by man. At the same time number control and territorial management of regional geographical populations is quite feasible through management of avian summer and winter habitats, as well as of territories along the major seasonal migration routes.

SUMMARY

Four groups of ethological mechanisms control seasonal distribution of avian populations as well as their flight paths; they are: (1) individual peculiarities of behavior; (2) experience acquired by individuals; (3) "collective experience" accumulated within local populations and maintained by learning of young birds from old ones; and (4) by innate reflexes of the total species and of its large geographical populations.

Innate reflexes determine choice of the main direction of seasonal migrations thus contributing formation of flight paths of the large geographical populations.

Individual experience is acquired by trial and error during an individual's life. The role of the period terminated by the first breeding season is of particular importance. The individual experience leads to emergence of birds populations having specific connections with breeding localities and habitats during the nonbreeding seasons.

ADAPTATION OF PREDATORY BIRDS TO ALTERED
ENVIRONMENTAL CONDITIONS

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The future existence of any group of birds, including the birds of prey,
depends on their ability or inability to adapt themselves to the current
changes in the surroundings, caused by human activities. Differentiative ana-
lysis of this ability is expected to allow estimation of the reasonable ex-
tent of anthropogenic impact tolerated by different species of predatory
birds. The results of such investigations would provide a basis for the ela-
boration and implementation of the most efficient strategy for managing the
predatory birds' surroundings.

In India more than ten years ago, I happened to observe an unique case of
a perfect adaptation of some birds of prey to the urban environment. The city
of Delhi harboured at that time as many as 3 thousand pairs of predatory birds
within 150 sq. km of its territory, including about 2,400 pairs of black ki-
tes, over 400 pairs of lappet-faced vultures, nearly 100 pairs of Egyptian
vultures, and odd pairs of other species. The average density of predatory
birds in the city was 19.3 breeding pairs per sq. km. The maximum density in
some large districts of the Old Town reached an incredible(for birds of prey)
figure of 70 pairs per sq. km. An extremely high density of breeding pairs
was reported in some settlements in the rural areas of northern India. The
well-being of the predatory bird populations in the city of Delhi can chief-
ly be accounted for by food abundance and - which is of an greater signifi-
cance-by the Indians traditionally favourable attitude to every living thing.

Peaceful co-existence of man and birds of prey seems to constitute the main
feature of life both in the countryside and in urban areas throughout India.
It testifies to the ability of these birds to adapt themselves to some inde-
structive forms of anthropogenic influence. It takes them, however, much more
time to overcome a deep-rooted fear of man as compared to passerine birds or
gulls, for that matter, which did not suffer such persistent victimization.
The Indian tradition of a benevolent attitude to every living creature is
thousands of years long while tolerance of predatory birds in this country,
in particular, dates back from the middle of the 1960s.

There are nevertheless prerequisites for the adaptive faculties of some
predatory birds to be revealed, their direct extermination having been dras-
tically reduced and sometimes completely abolished by the current protective
measures.

Evidence to this effect has been obtained all over the world, including
our country.

In the middle of the 1960s and 1970s we carried out a comparative survey
of a region about 150 km east of Moscow using identical techniques. Over ten
years, the number of six breeding species of predatory birds increased here
from 23.3 to 27.5 pairs per 100 sq. km of woodlands, i.e. by 18% on average.
The common buzzard, sparrow-hawk, goshawk, and kestrel were the species that
had mostly contributed to this increase.

A similar tendency to an increased or maintained population density of predatory birds has been observed in many other regions in our country; this ground can be covered by specialists who dealt with this problem there. It is important to emphasize, however that this trend is valid chiefly or exclusively in so far as the number of rather common birds are concerned, e.g. the common buzzard, pern, goshawk, sparrow-hawk, hobby falcon, all the harrier species, long-eared and march owls, and sometimes black kite process to be currently underway in many European and North American countries.

There is quite a different and, in fact, situation as regards rare predatory birds - entries to the USSR Red Data Book or the Red Data Books of the Soviet Union Republics. The number of these birds in many regions keep decreasing. In-depth studies of this process and its causes were undertaken in Estonia using the peregrine population as a model. Against this background there are encouraging reports published in the last two or three years on the renewal of some aeries of the peregrine, golden and white-tailed eagles as well as bearded vulture. These are, however, but rare instances.

The differences in the present-day status and trend in the numbers of these droups of predatory birds - rare and rather common - appear to testify to their different response to a variety of anthropogenic factors.

The majority of species can be subdivided roughly into two groups according to their response to a direct destruction by man, which has the most deleterious effect upon the populations. A significant lessening of this influence in the late 1960s and early 1970s brought about a somewhat positive sequel for a number of birds while it failed to affect the others.

The first group embraces many common birds of prey that are known to be perfectly adapted to the limited alterations of the landscape caused by man (common buzzard, pern, hawks, harriers, hobby falcon, and presumably some others). Some of these birds have been shown to distinguish people as safe or dangerous by their appearance or behaviour. This ability is to be regarded as indicative of the adaptive faculty in these birds. Of no small account is the fact that many birds of prey are capable of living under the pressure of the habitual anthropogenic disturbance, but do not sustain its sudden impact. On the whole the species in this group are not expected to be negatively affected by man's presence.

The second group compises rare species, which are highly susceptible to an impact from any modification of their surroundings. These birds are least of all resistant to human impact.

Many species cannot be classed with group and are supposed to occupy an intermediate position as the data on their status are far from sufficient.

This tentative scheme makes it possible to appraise the prospects for each group of birds and elaborate the appropriate measures for maintaining their optimal living conditions in the future.

The species in the first group are expected to enjoy their adaptive capability to the utmost, provided that the modern legislation protecting all birds of prey from extermination will remain in force for an infinitely long time. Populations of these birds would grow progressively until the ecological capacity of their habitats is saturated. The existence of their viable populations under conditions of rapid socio-economic development does not seem to

require any special governmental measures except for strict enforcement of the legislation on nature conservation and ecological decorum whenever a man gets in touch with Nature.

Survival of the second group of birds is still doubtful unless urgent measures are taken to this effect. Special programmes are needed to prevent their extinction. They should envisage setting up protected areas wherever breeding grounds of rare species are preserved, conserving separate aeries, erecting artificial platforms to support nests, establishing feeding points, and breeding birds in open-air cages to secure an emergency genetic fund and subsequent release of the young birds to revive failing populations. Measures to prevent the mortality of predatory birds caused by pesticides and by stumbling on overhead power transmission lines are of primary importance. Efficient nature protection and conservation are the two main approaches to ensure the existence of birds of the second group.

One should bear in mind that most common species in the first group have been victimized by man for a relatively short span of 100 to 150 years, while the rare species in the second group have been suffering human impact for many centuries. Golden and white-tailed eagles are known to have been killed in Europe from as early as the 16th century on the pretext of their preying on lambs. Nestlings of large falcons have been collected from aeries for the purpose of falconry from time immemorial. Shy individuals avoiding contacts with man appear to have survived in the process of natural selection in populations of this birds.

To sum up, the following conclusions can be drawn from the foregoing. Reasonable transformation of the natural environment does not preclude normal existence of predatory bird populations. As birds are gradually getting the better of their shyness, their adaptive potencies, hampered by all kinds of human destructure activities, are supposed to be revealed making it possible for the populations to adjust themselves to present-day or future levels of anthropogenic influence. Strict enforcement of the current legislation protecting birds of prey and implementation of special programmes for the management of rare species are major prerequisites for this trend to continue.

It can be inferred that measures to be taken to secure optimal conditions for birds of prey are not in conflict with society's socio-economic progress.

We have good reason to consider the last decade and the present moment in particular to be the turning points in the dynamics of the status and numbers of predatory bird populations.

It is up to us to determine whether this favourable trend will continue and how rapidly.

There are still many problems of concern, but we have also good reason to be optimistic, all the more so that I can see a lot of young faces here both among those presenting reports and those listening to them.

I am sure that birds of prey do have genuine friends to take care of their well-being in the future.

SUMMARY

Future of raptors depends on their ability to adapt themselves to environmental changes mostly induced by man. There are extreme examples of both full adaptation of raptors to living in big cities (for instance, about three thousand breeding pairs in Delhi, India) and entire disappearance of some species from great regions. In recent years the most negative forms of man's impact upon raptors, i.e. direct persecution, pesticides, nest destruction etc. are weakened. Therefore a study of such relatively moderate forms as habitat changes, disturbance, influence on food supply and so on becomes important to ensure a stability and increase of their populations.

According to adaptive capability to modified environment, raptors can be divided into two provisional groups: 1) relatively tolerant to man's activity, i.e. common buzzard, honey buzzard, sparrowhawk, goshawk, harriers, hobby and some others; 2) intolerant to man's presence, i.e. most of rare species like eagles, big falcons, vultures, osprey and others. Some species occupy intermediate position (black kite and kestrel in our conditions) or their attitude to a man is unknown.

Species of the first group react positively when persecution and other severe forms of negative influence are abolished. In many regions of the USSR after a legislative act in the middle of sixties their populations became stable or increased slightly. To be fully adapted to a modified environment, raptors of the first group need some measures, mostly local, to soften disturbance of them especially during nesting period.

Raptors belonging to the second group could not exist in a changing environment without a special programm of their conservation which includes establishment of permanent or temporary reserves, help in nesting and feeding, strict protection against disturbance and other measures as well as captive breeding for reintroduction of rare raptors to the wild.

# PROBLEMS OF GOSHAWK PREDATION ON PIGEONS AND OTHER GAME

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## INTRODUCTION

Raptors have long attracted man's antipathy for killing poultry, and seve-
ral species gained the local or even national name of "chicken-hawk". In more
modern times, raptor predation on game has caused considerable concern. At-
tention has focussed especially on the Goshawk (Accipiter gentilis), because
its numbers have recently increased in several parts of Europe (Kalchreuter,
1981; Thissen et al., 1981; Marquiss, Newton, 1982) and it takes more game
than most raptors. This paper reviews some past studies of raptor predation
on game, describes recent results obtained by radio-tracking Goshawks, and sug-
gests ways of approaching predation problems in the future.

## A PAST VIEW OF PREDATION

For the last 40 years our view of predation has been strongly influenced
by the work of Paul Errington. From studies of Muskrat (Ondata zibethica) and
Bobwhite Quail (Colinus virginianus), Errington (1946) concluded that predat-
ion was unimportant in population regulation of herbivores because its victims
were "so often the immature, the ill-situated, the restless, the wanderers or
the otherwise handicapped" and that predation therefore merely compensated for
other types of population loss. Many other studies showed that raptors tended
to select weak or "odd" prey (Dice, 1947; Eutermoser, 1961; Pielowski, 1961;
Mueller 1974), but Errington's study and the later work on Red Grouse (Lago-
pus lagopus scotticus) by Jenkins et al. (1964) put this selection into the
context of population dynamics. The view became established that predators
take mainly the "doomed surplus" from prey populations.

The idea that raptors have little long term impact on game populations was
supported by the first extensive studies of raptor communities and their food
supply. Craighead, Craighead (1956) estimated that a North American raptor
guild killed only 5-18% of the autumn game bird populations, and accounted for
18% of the total Pheasant (Phasianus colchicus) winter mortality. Brüll (1964)
concluded that raptors in Northern Germany took too few Pheasants and Partrid-
ges (Perdix perdix) to affect their breeding populations. The territorial be-
haviour found in Buteo species (Fitch et al., 1946; Dare, 1961) and Tawny Owls
(Strix aluco) (Southern, 1970) was assumed to restrict the foraging areas of
many raptors, so that their numbers would not usually build up to increase
predation pressure in an area unless resident raptors were removed (e.g. shot
or trapped). Evidence was accumulating that bird populations were limited by
their food supply, not by predation (Lack, 1954, 1966). The views were there-
fore promoted that raptors could not reduce game populations, that they might
sometimes act as beneficial "health police" by rapidly destroying diseased
prey (Leopold, 1933), and that resident raptors should be preserved because
they would keep others out of their territory (Brüll, 1964) and avoid taking
prey near their nests (Schnurre, 1935).

# TECHNIQUES FOR STUDYING GOSHAWK PREDATION

Past assessments of Goshawk predation have been based on diet studies, using pellets (Uttendorfer, 1952), direct observations and prey remains at nests (Siewert, 1933; Sulkava, 1964; Schnurre, 1965; Wikman, 1977), kills found by searching (Brüll, 1964; Göransson, 1975; Opdam et al., 1977) or stomach contents from killed hawks (von Bittera, 1915; Höglund, 1964; Marcström, Widén, 1977). Sources of error in these techniques are well known (Errington, 1932; Einarsson, 1956), and can seriously bias the proportion of game recorded in the diet. For instance, Ziesemer (1981) showed that, compared with radio-tracking, visually searching an area for prey remains may record all the pale-coloured pigeon kills, but only one third of the Pheasants and one eighth of the Rabbit (Oryctolagus cuniculus) remains. On the other hand, stomach content analysis may overestimate predation on poultry and game if hawks are killed mainly at farms and game reserves. Goshawk pellets are extremely difficult to find away from nests, because hawks seldom roost regularly in one place unless they are exploiting prey which are abundant in a small area; in this case pellets too may not represent the general diet.

Another problem with using diet to assess predation is that estimates of hawk food requirements and wastage are needed to convert dietary frequencies into kill-rates. Moreover, unless fresh prey carcases are available, there can be only a limited investigation of whether poor quality prey is being selected. Observation at nests enables direct measurement of kill-rates, and some selection analysis (Sukava, 1964; Perrins, Geer, 1980; Geer, 1981), but records mainly male prey for much of the season, and not necessarily the diet of non-breeding males and females, nor of breeders if many prey are eaten away from the nest (Newton, Marquiss, 1982), nor of hawks at other times of year.

These problems can be overcome by radio-tracking hawks or their prey. Both techniques entail direct measurement of kill-rates and facilitate recovery of fresh kills. Tracking prey provides data on all sources of prey mortality (Dumke, Pils, 1973), but requires large numbers of transmitters, which must not themselves increase prey vulnerability to predation (Msch, 1967). Tracking hawks requires fewer transmitters, enables the most immediate analysis of fresh carcases, and provides additional data on hawk density, behaviour, mortality and nest locations (Dietrich, Ellenberg, 1981; Kenward et al., 1981; Widén, 1981, Kenward, 1982; Ziesemer, 1982), but biases against recording relatively small prey. The technique is ideal for assessing Goshawk predation on animals weighing more than about 250g (i.e. game). However, compared with stomach analysis, fewer than half the smaller prey may be recorded if hawks are monitored less than about once an hour (Kenward et al., 1981). More continuous monitoring means data from fewer hawks. Even concentrating entirely on predation at the expense of other information, and monitoring several hawks equipped with special transmitters which indicate when they are feeding (Kenward et al., 1982), one would not expect to record more than about one Goshawk kill per observation day.

## RECENT STUDIES OF GOSHAWK PREDATION

### Predation on Woodpigeon populations: the effects and mechanism of selection

The Woodpigeon (Columba palumbus) can cause serious damage to brassica and

pea crops in Britain (Murton, 1965). In 1971 I started to investigate whether the Goshawk, which was recolonising Britain (Marquiss, Newton, 1982), could help to prevent this damage, either by reducing pigeon numbers or by scaring pigeons from vulnerable crops.

Hawks marked with tail-mounted radio-transmitters (Kenward, 1978a) were released in a lowland area with much brassica cultivation, and followed individually to record their kills. The bodyweight of captured pigeons was estimated from one supracoracoideus (pectoralis minor) muscle, which could usually be excised intact from part-eaten carcases and correlated very strongly ($r_{105} = 0.897$) with bodyweight (Kenward, 1978b); there was no correction for bodysize because variation in sternum+coracoid span accounted for only 7% of bodyweight variation. Compared with pigeons shot at roosts of the local population, Goshawks showed selection for birds of below average bodyweight, but not for any particular age or sex category outside the pigeon breeding season (Table 1).

If the hawks had killed only the thinnest pigeons, the predation would have had a negligible effect on the population size, because most such birds were dying anyway. The observed selection was more subtle, however, with some high bodyweight pigeons being killed, but low weight birds being taken more frequently relative to their presence in the population. The degree of compensation for other mortality associated with low weight (e.g. food-shortage, disease) could be estimated from Woodpigeon marking data collected in similar habitat but without Goshawk predation by Murton et al. (1971). As a survival index, the probability (y) of resighting a pigeon of bodyweight (x) more than one month after marking in mid-winter (correcting for emigration) was:

$y = 0.0019x - 0.60$ for adults, and

$y = 0.0012x - 0.28$ for juveniles.

Using these equations, the mean survival prospects of pigeons captured by the hawks were 72% those of shot samples. Thus if the hawks killed 100 pigeons, their net removal from the population at that time would have been 72, because 28 would have soon died away.

As well as removing pigeons that were already dying, the hawks were also killing pigeons which might subsequently have suffered food-shortage. This meant that although a pigeon was killed every four "hawk-days", a natural Goshawk population would have been able to reduce the large lowland Woodpigeon population substantially below the limiting February food supply (Murton et al., 1964, 1966) only at winter Goshawk densities above $0.4$ hawks/$km^2$. Such Goshawk densities do occur, but have only been recorded in areas with high

T a b l e  1. The sex and estimated bodyweight (g) of Woodpigeons captured by Goshawks or shot in Oxfordshire between November 1974 and March 1975

| | Sex structure | | | | Adults | | | Juveniles | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Sex subtotals | | | | Bodyweight | | | Bodyweight | | |
| | Total | Fsmale | Male | ? | N | Mean | Range | N | Mean | Range |
| Captured | 21 | 8 | 7 | 6 | 14 | 471 | 396-579 | 5 | 443 | 342-317 |
| Shot | 38 | 19 | 17 | 2 | 22 | 540 | 415-589 | 16 | 528 | 487-587 |

densities of released Pheasants (see later). Removal of pigeons in early winter might also have left more food for February, and thus increased their breeding population (Lack, 1954).

To investigate the value of hawks for scaring Woodpigeons from vulnerable sites, a Goshawk trained for falconry was flown at flocks feeding on winter brassicas. Large flocks were difficult for the hawk to approach undetected, so that the bird eventually showed some reluctance to attack them, and the pigeons often resettled on their food immediately after an attack. Approaching humans were slightly (but not significantly) more effective for scaring pigeons away than was a hawk attack (Kenward, 1978c). Although pigeons would not settle while a hawk soared nearby, the actual attacks were of little value for scaring them, but did provide data on selection mechanisms.

Attacks were most successful at small flocks and single pigeons, partly because the approaching hawk was detected earlier when more pigeons were present and partly because singletons were often too weak to outfly the hawk (Kenward, 1978b). Woodpigeons could normally outfly the Goshawk if they took off when it was more than about 20m away, so early detection of the predator was important for the prey. If the pigeons took off with the hawk close at hand there was often a chase, and it was then that selection of weak pigeons occurred, because the hawk caught those that lagged behind. When the hawk surprised the pigeons where they sat, the condition of those taken represented a random cross-section of bird in the flocks (Figure 1). Selection of poor quality pigeons thus occurred only after a chase. This effect was apparent among pigeons killed by the radio-tagged hawks too, because 7 birds taken in or near cover, where surprise was likely, had significantly higher weights than 3 killed in open fields (P = 0.04).

## Predation on Pheasants: the response to prey availability

To investigate predation on Pheasants (Phasianus colchicus) by a wild Goshawk population, hawks were trapped and radio-tagged initially at a Swedish estate where more than 4,000 captive reared Pheasants were released annually (Kenward, 1977). Since Goshawks took 1-3 hours for their first meal on a Pheasant, and subsequently returned until the carcase was cleaned of meat or scavenged, up to six hawks could be monitored at a time by checking each at 1-2 hour intervals to see if it had killed. This resulted in some kills of small prey being missed, but provided many more data on Pheasant predation than if single hawks had been followed continuously: few, if any, Pheasant kills would have been missed. A Pheasant was killed, on average, every 1.7 hawk-days in August and 2.3 hawk-days in October. The kill-rate declined to 3.6 and 8.7 hawk-days per Pheasant in December and January, respectively, after the prey population had been substantially reduced by shooting, trapping up breeding stock and hawk predation.

The number of hawks hunting in the study area could be estimated by using the radio transmitters as markers in a modified Lincoln-Index calculation. All hawks seen while not being radio-tracked were immediately checked for the presence of a transmitter. The total number present was derived from the ratio of radiotagged to untagged hawks seen when a known number of tagged hawks were present. The validity of the estimate was confirmed by Pheasant kills
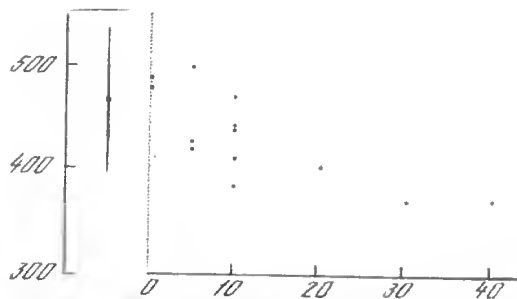
F i g. 1. The bodyweight of Woodpigeons captured by a Goshawk from flocks at brassica sites, compared with the mean (±1 and 2 x S.C.) for pigeons shot from flocks at the same sites. Low bodyweight pigeons were selected when a chase occurred

found independently by the gamekeepers: the ratio of tracked hawk kills to "unknowns" was the same as the ratio of tagged to untagged hawks in sightings Knowing also the proportion of the radio-tagged hawks' time which was spent in the study area, and assuming the same for untagged hawks, the average density of all hawks in the area was estimated during October, when the released pheasants had reached full size but before numbers had been reduced by shooting.

The total predation on Pheasants in the area, given by (the average killrate per radio-tagged hawk) x (the number of hawks hunting the area), was about 1% of the released birds (40 Pheasants) per week in October, and would not have been less earlier in the autumn when the predation rate was higher. This 1% per week may underestimate the potential loss of game, because 11 of 23 trapped hawks had been removed from the estate in the previous 2 months to preserve more Pheasants for shooting.

The large number of hawks present reflected a total lack of territoriality. The ranges of five radio-tagged males were essentially superimposed, rather than overlapping at the edges, and the area used by all five (encompassing 8 of 9 Pheasant feeding sites) was used by them 3-5 times as frequently as expected if they used all parts of their ranges equally. Occasional mildly aggressive encounters were seen between hawks, but in this and subsequent studies they never resulted in radio-tagged hawks leaving an area.

Similar work was done in a wild-Pheasant study area, censusing the Pheasants in autumn and spring to estimate the over-winter loss (Kenward et al., 1981). Goshawks killed Pheasants much less frequently than at the estate with released game, but female Pheasants in particular suffered a high winter mortality, of which 88% was due to Goshawks (Table 2). Male Pheasants were killed mainly by shooting, which was directed at the cocks to preserve hens for breeding. The female Pheasants were reduced to a level at which they could only have reproduced the original autumn population by breeding at the single highest rate (4 young per hen) recorded in four study years of three Scandinavian Pheasant populations (Göransson, 1980). In fact the Pheasant population has declined to near extinction in this study area, with no marked changes in land use during the last decade. The most likely cause was the Goshawk predation.

T a b l e 2. The contribution of Goshawk predation and shooting to winter mortality of wild Pheasants at an estate in central Sweden

| Pheasant sex | Total overwinter loss (%) | Cause of loss between censuses | | |
|---|---|---|---|---|
| | | Goshawk (%) | Shooting (%) | Unknown (%) |
| Male | 76 | 23 | 69 | 8 |
| Female | 64 | 88 | 8 | 4 |
| Total | 71 | 50 | 43 | 7 |

Supracoracoideus muscles were used to estimate bodyweight of killed Pheasants in both these studies, correcting to a standard bodysize because variation in sterno-coracoid span accounted for 34% of bodyweight variation in full-grown cocks and 23% in hens. Hawks showed no significant selection of hen Pheasants with lower bodyweight compared to those shot at roosts and during drives, or trapped, at the two estates (Table 3), although in one compa-

T a b l e 3. The size-corrected bodyweight (g) of Pheasants captured by Goshawks, shot, or trapped between October and March at two estates in central Sweden

| | Captured by hawks | | | Shot or trapped | | |
|---|---|---|---|---|---|---|
| | N | Mean | Range | N | Mean | Range |
| Released Pheasants: | | | | | | |
| Females, shot or captured at same release sites between October, December | 22 | 957 | 758-1110 | 298 | 967 | 701-1200 |
| Males, shot or captured at same release sites in October | 3 | 906 | 650-1106 | * 6 | 1109 | 1031-1116 |
| Males, shot or captured at different sites in January | 4 | 1294 | 1226-1388 | 43 | 1288 | 1047-1500 |
| Wild Pheasants: | | | | | | |
| Females, trapped or captured between October, March | 11 | 972 | 854-1064 | 23 | 984 | 799-1190 |
| Males, trapped or captured between October, March | 5 | 1311 | 1215-1413 | 5 | 1242 | 1120-1342 |
| Males, shot or captured between October, March | 5 | 1311 | 1215-1413 | 13 | 1307 | 1090-1450 |

* Difference significant, P = 0.05; no other significant differences.

rison there was evidence for selection of low weight cocks. This does not mean
that no selection for low bodyweight occurred among hens, because any preda-
tor must occasionally benefit from prey weakness and there may have been some
selection in shooting or trapping (though probably not in roost shooting),
but this selection was certainly much less marked than in Woodpigeons. The
reason for this species difference is indicated by the Pheasant feeding beha-
viour and escape tactics when attacked. Pheasants seldom fed more than about
10m from cover, into which they ran or flew when a hawk appeared, and only
4% of 79 kills were more than 5m from cover (with another 14% in light cover
which would not have protected them but could have hindered their view of an
approaching hawk). These observations showed that, if hawks did not surprise
the Pheasants, the prey could easily escape without a chase in which selec-
tion for weakness could have occurred.

In this strongly dimorphic prey, however, a marked selection of hens de-
veloped during autumn, in the area with released Pheasants (Table 4), des-
pite a 1:1 sexratio maintained from release to first shooting in mid-Novem-
ber. With Pheasants in groups, the hawks probably chose to attack hens be-
cause they are smaller and easier to subdue than cocks. Similar selection of
hens among wild Pheasants developed during snowcover, but this has not been
found among Pheasants killed by Goshawks elsewhere (Göransson, 1975; Marc-
ström, Widén, 1977; Ziesemer, 1982), possibly because hawks can only choose
hens when (a) Pheasants are very abundant, or (b) the camouflage of hens is
rendered less effective by snow.

Goshawk predation on Pheasants has also been studied by radio-tracking in
two areas of northern Germany (Ziesemer, 1982) and in three more areas of
Sweden, all with fairly similar habitat. Thus data from seven areas are now
available from which to investigate the Goshawk response to changes in the
density of this one prey.

The functional response of the average individual kill-rates (Figure 2)
is a typical "Type 2" response (Holling, 1959), the limiting "handling time"
being the rate of predation needed to obtain all food requirements from Phea-
sants. A Pheasant provides 3-4 days of food for a Goshawk (Kenward, 1977),
equivalent to a limiting kill-rate of 0.25-0.33 Pheasants per hawk-day, but

T a b l e  4. Selection of female Pheasants by Goshawks at two estates in
central Sweden

| | Number captured by hawks | | | |
|---|---|---|---|---|
| | Male | Female | | % Female |
| Released Pheasants: | | | | |
| August | 10 | 5 | | 33 |
| October | 25 | 51 | *** | 67 |
| November | 1 | 14 | | 93 |
| Wild Pheasants: | | | | |
| During snowcover | 2 | 19 | | 90 |
| Without snowcover | 4 | 2 | ** | 33 |

*** Trend significant, $P < 0.001$; ** difference significant, $P = 0.011$.

672

F i g. 2.
The functional response of Goshawk
kill-rates to change in Pheasant
density
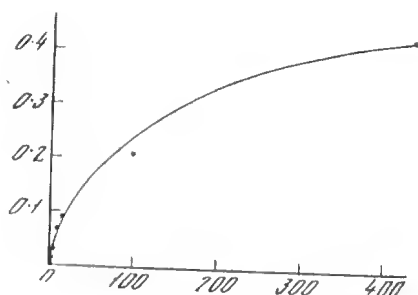
kill-rates were increased by scavengers removing carcasse (mainly Red Fox
<u>Vulpes vulpes</u>) at the two sites with greatest Pheasant density. The rates
shown for these two sites are the autumn rates, because prey densities and
predator kill-rates subsequently declined more than at the other sites,where
kills and hawk sightings were too few to produce separate autumn and winter
estimates. Variation in habitat between areas should alter Pheasant vulnera-
bility and hence availability ((f) density vulnerability) to the predator,
creating variation in the kill-rate at a given density, but this would pro-
bably not affect the general shape of the response curve. There was no evi-
dence of a switch to predation on Pheasants as their density increased,which
would give rise to a sigmoid "Type 3" response, probably because Pheasants
were a preferred prey at any density. Wikman, Linden (1981) showed a similar
strong convex functional response by breeding Goshawks to Woodland Grouse
(<u>Tetraonidae</u>) density, as found for other breeding raptors by Keith et al.
(1977), but responses by wintering raptors have generally been weaker (Phe-
lan, Robertson, 1978).

    As in other raptor studies (Galushin, 1974, review in Phelan, Robertson,
1978), there was a strong Goshawk numerical response to changes in prey den-
sity (Figure 3). Two functions are shown, one based on the autumn hawk den-
sity observed (O) at the site with most Pheasants and one based on the den-
sity predicted (P) if the 11 hawks removed from the site had used the area
as much as those radiotagged and released on site. The response appears to
be sigmoid (Type 3), as found in some other field studies of vertebrate pre-
dation (Holling, 1959; Goss-Custard, 1970), but it is impossible to be pre-
cise about the shape of the function without more data for high and interme-
diate Pheasant densities. Enhanced Goshawk densities may occur at low Phea-
sant densities if other prey are abundant, as in a Swedish area (*) where
Rabbits were 71% of 56 recorded prey.

    Figure 4 shows estimates of total predation on Pheasants for six areas
(no Pheasant kills were recorded in the seventh). Values of 5-6% of the Phea-
sant population per month are equivalent to the highest losses recorded bet-
ween seasons, of 34 and 35%. Total predation was very variable, and could be
as great at low as at high Pheasant densities. Predation was particularly
high in the area with abundant Rabbits, which appeared to draw in hawks (Fi-
gure 3) and thus increase predation on Pheasants instead of acting as a "buf-
fer" (Leopold, 1933). Perhaps an increase in alternative prey only reduces
predation on species which are less vulnerable than the alternative.
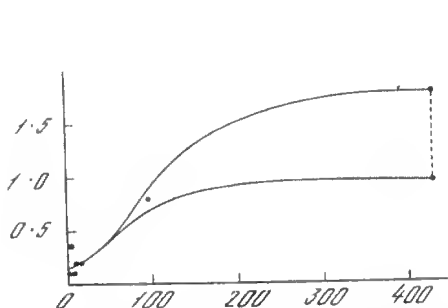
F i g. 3. The numerical (gathering) response of Goshawks to change in Pheasant density.Rabbits were a very abundant alternative prey at one site(*)
F i g. 4. The total predation of Goshawks on Pheasants at different prey densities
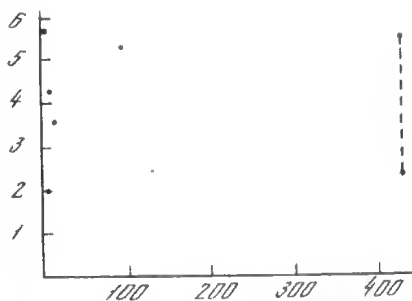
DISCUSSION

As a simplification, three degrees of intensity can be distinguished in the impact of a predator on its prey. The first occurs when the predation is entirely compensatory for other density dependent mortality, such as winter food-shortage, and the prey breeding population is not reduced. Second degree predation is intense enough to reduce the subsequent breeding population to a lower level, and third degree predation produces a continued decline to the extinction of the prey. The category found will depend both on prey vulnerability and on predator density. If prey is only vulnerable when young or in poor condition, or predators are very scarce, only $1^o$ predation is likely (Errington, 1946). If prime prey is vulnerable in some locations, for example when far from cover, then $2^o$ predation is possible if there are enough predators, but a limit may be reached if prey vulnerability decreases (e.g. due to experience avoiding predators or less need to feed out of cover) as prey numbers fall (Gause, 1934; Schnell, 1968). Third degree predation is possible only if prey are very vulnerable or relative predator density is very high.

Predators are liable to extinction during $2^o$ or $3^o$ predation unless there is alternative prey,although local prey extinctions can occur without predator extinction if there are many prey subpopulations with some movement of predators between them (Huffaker, 1958).

This categorisation helps in considering the impact of predation, but is artificial in the sense that continuous variation in predator density and prey vulnerability imply continuous variation in predation pressure. There is also no consideration of variation in the availability of alternative prey, which may influence predator density and compete for predator attention with the investigated prey.

Although a number of recent studies have shown that predators can markedly reduce the number of young birds produced, this has still mainly been found not to greatly reduce the size of subsequent breeding populations (Duebbert, Lokemoen, 1980; Perrins, Geer, 1980; Potts,1980): it is $1^o$ predation. There is far more evidence of bird populations being limited by their food.supply (Newton, 1980), and most predation on birds is $1^o$.

Evidence for temporary or permanent prey population reduction, $2^o$ predation, has so far been found mainly among mammal prey. Pitelka et al. (1955) recorded very heavy predation by Skuas (Stercorariidae) and Owls (Strigidae)

674

on a peak Lemming (_Lemmus_ sp.) population, and believed that the predators caused the subsequent decline. Later authors did not consider predation likely to limit peak populations in fluctuating (or "cyclic") prey, but have shown how predators can temporarily reduce mammal populations below the limit of food supply when prey numbers are low (Pearson, 1966, Keith, Windberg, 1978). More permanent 2° predation effects have usually resulted from removal (Gibb et al., 1980; Marcström, 1982) or establishment of predators (Mech, 1970; Powell, 1980), although differences in prey populations have also been recorded in areas with naturally differing predator pressure (Kruuk, 1970). Lack of similar data for bird populations probably reflects (i) the ability of adult birds to fly away from mammalian predators, and (ii) the depressed state of raptor populations in temperate countries (Lack, 1954), where most studies have been done, because of persecution and pesticides.

A number of island birds and mammals have become extinct because of extreme vulnerability to introduced predators (Elton, 1958). Although this 3° predation seems unlikely between species have co-existed for millenia, it could happen to prey which are rendered unusually vulnerable by habitat degradation, and perhaps also locally during predator "invasions". For instance, Goshawks prey heavily on Ruffed Grouse (_Bonasa umbellus_) in North America, depressing Grouse numbers near Goshawk nests (Eng, Guillion, 1962), and may cause local extinctions (M.R.Fuller, pers. comm.) during major southward Goshawk irruptions (Mueller et al., 1977). These mainly juvenile Goshawks may then starve, but their breeding population will survive in the north (and Grouse presumably re-establish themselves from less affected areas).

## Goshawk predation on Pheasants

Goshawk predation on Swedish Pheasants was first studied in a southern study area by Göransson (1975). From prey remains he estimated that hawks took 25% of the population in one winter, accounting for 75% of the mortality, but only 8% (19% of the winter mortality) the next year. He suggested that Pheasants were particularly vulnerable the first year because of illness among them, and that Goshawks would normally take only 10-15% (with hunters obtaining 30-35%).

The data on wild Pheasants in central Sweden (Table 2) indicate 2° predation, perhaps leading to local extinction (3°). The high predatory impact was explained partly by the vulnerability of the Pheasants, which showed no signs of disease but were a preferred prey even at low density (Figure 2), and partly by the gathering ability of Goshawks (Figure 3) with no evidence of territoriality. In more southern parts of Europe, the predation may be less because of better cover and a less mobile Goshawk population, which is not re-inforced during winter by immigration from the north, as in southern Fennoscandia (Marcström, Kenward, 1981). Predation might also be reduced in areas with more alternative prey, but the role of Rabbits at one study area (Figures 3, 4) indicates that a greater food supply may also increase Goshawk density and thus increase predation on Pheasants unless alternative prey is also more vulnerable than Pheasants. Research is needed in more areas where Goshawks are thought to damage stocks of game. Using radio-tracking techniques to estimate autumn kill-rates and hawk densities need not take more than 2-3 man-months,

and would gradually reveal much more about Goshawk predation mechanisms.

Pheasants are introduced in northern Europe, but their high vulnerability
to Goshawks is probably not explained by a lack of natural defence against
this predator, because Goshawks are found in the original Pheasant range. On
the other hand, Pheasant vulnerability is probably greatly increased by the
destruction of cover in modern farming (Göransson, 1980). Several suggestions
have been made for improving cover and reducing Goshawk hunting opportunities
at sites favoured by Pheasants (Kenward, Marcström, 1981; Ziesemer, 1982),and
this may be enough to prevent Goshawks reducing Pheasant breeding numbers in
most areas. Of course, the hawks may still be a problem for hunters by compet-
ing for the harvestable post-breeding surplus. Where Goshawks are common
enough for serious competition with hunters, however, their national breeding
population is unlikely to suffer if the local density is reduced in a few
areas (and see Haukioja, Haukioja, 1970). Live-trapping with spring-nets on
Pheasant kills is then to be recommended, because it is selective of hawks
killing Pheasants (Kenward et al., 1983), and trapped birds can be released
elsewhere if required: few return if released more than 30 km away (Marcst-
röm, Kenward, 1981).

SUMMARY

1. Early studies of raptor predation indicated that raptors could not re-
duce prey breeding populations and might even assist game management. These
studies mostly derived kill-rates by combining diet analysis, which can pro-
duce biased estimates of predation on game, with assumptions about raptor
food requirements and wastage.

2. Radio-tracking enables direct measurement of kill-rates, examination
of fresh kills for selection effects, and can also be used to estimate rap-
tor densities outside the breeding season.

3. Goshawks radio-tracked in Britain selected low weight Woodpigeons,which
reduced the predatory impact on this prey. Arranged attacks on pigeons flocks
showed that this selection depended on the occurrence of a chase, and that
pigeons with normal bodyweight were taken when a hawk surprised them.

4. Goshawks tracked in Sweden did not select poor quality Pheasants, whose
escape behaviour provided little chance of a chase, but apparently chose to
attack hens rather than cocks when possible. Hawk predation on wild Phea-
sants was very heavy, and was probably reducing their breeding population.

5. The Goshawk functional response to changing Pheasant density in Swe-
dish and German studies indicated that Pheasants were a preferred prey in
these areas, and hawks accumulated where Pheasants were abundant, causing
serious competition with hunters for this game. High availability of alter-
native prey in one area did not "buffer" the Pheasants against Goshawk pre-
dation, but increased predation on them by increasing hawk density.

R e f e r e n c e s

Brüll H. Das Leben deutscher Greifvögel. Stuttgart: Fischer, 1964.

Craighead J.J., Craighead F.C. Hawks, ols and wildlife. Wildl. Mgmt. Inst., Wash., 1956.

Dare P.J. Ph.D. Thesis. Univ. Exeter., 1961.

Duce R.L. - Cont. Lab. Vert. Biol. Univ. Mich., 1947, 34, p. 1-20.

Dietrich J., Ellenberg H. -In: Understanding the Goshawk / Eds. R.E.Kenward, I.Lindsay. Int. Ass. Falconry Cons. Birds of Prey, 1981, p. 163-175.

Dumke R.T., Pils C.M. - Dept. of Natural Resources, Wisconsin, Tech. Bull., 1973, 72, p. 52.

Duebbert H.R., Lokemoen J.T. - J. Wildl. Mgmt, 1980, 44, p. 428-437.

Einarsen A.S. Determination of some predator species by field signs. Oregon State Monographs 10, 1956.

Elton C.S. The Ecology of Invasions. L.: Methuen, 1958.

Eng R.L., Gullion G.W. - Wilson. Bull., 1962, 74, p. 227-242.

Errington P.L. - Condor, 1932, 34, p. 75-86.

Errington P.L. - Quart. Rev. Biol., 1946, 21 (2), p. 144-177; 21 (3), p. 221-245.

Eutermoser A. - Vogelwelt, 1961, 82, p. 101-104.

Fitch H.S., Swenson F., Tillotson D.F. - Condor, 1946, 48, p. 205-237.

Galushin V.M. - Ibis, 1974, 116, p. 127-134.

Gause G.F. - The Struggle for Existence. N.Y.: Hafner, 1934.

Geer T. -J. Zool, Lond., 1981, 195, p. 71-80.

Gibb J.A., Ward C.P., Ward G.D. - D.S.I.R. Bull., 1978, 223.

Göransson G. - Anser, 1975, 14, p. 11-22.

Göransson G. Ph.D. Thesis, Lund University, 1980.

Goss-Custard J.D. - J. Anim. Ecol., 1970, 39, p.91-113.

Haukioja E., Haukioja M. - Finnish Game Res., 1970, 31, p. 1-20.

Höglund N.H. - Viltrevy, 1964, 2 (5), p. 271-328.

Holling C.S. - Can. Entomologist, 1959, 91, p. 293-320.

Huffaker C.B. - Hilgardia, 1958, 27, p. 343-383.

Jenkins D., Watson A., Miller G.R. - J. app. Ecol., 1964, 1, p. 183-195.

Kalchreuter H. - In: Understanding the Goshawk / Eds. R.E.Kenward, I.Lindsay. Int. Ass. Falconry Cons. Birds of Prey, 1981,p. 18-28.

Keith L.B., Todd A.W., Brand C.J. et al. - In: Proc. XIII Cong. Game Biol. L., 1977, p.151-175.

Keith L.B., Windberg L.A. A demographic analysis of the snowshce hare cycle. Wildlife Monographs 58, Wildlife Society, Wash. DC, USA, 1978.

Kenward R.E. - Viltrevy, 1977, 10, p. 79-112.

Kenward R.E. - Ornis Scand., 1978a, 9, p.220-223.

Kenward R.E. - J. Anim. Ecol., 1978b, 47, p. 449-460.

Kenward R.E. - Ann. appl. Biol., 1978c, 89, p. 277-286.

Kenward R.E. - J. Anim. Ecol., 1982, 51, p. 69-80.

Kenward R.E., Hirons G.J.M., Ziesemer F. - Symp. Zool. Soc. Lond., 1982, 49, p. 129-137.

Kenward R.E., Marcström V. - In: Understanding the Goshawk / Eds. R.E.Kenward, I.Lindsay. Int. Assoc. Falconry and Cons. Birds of Prey, 1981, 152-162.

Kenward R.E., Marcström V., Karlbom M. - J. Wildl. Mgmt, 1981, 45, p. 397-408.

Kruuk H. - In: Animal Populations in relation to their food resources / Ed.
    by A.Watson. Symp. Brit. Ecol. Soc. 10, 1970, p. 359-374.
Lack D. The natural regulation of animal numbers. Oxford Univ. Press, 1954.
Lack D. Population studies of birds. Oxford Univ. Press, 1966.
Leopold A. Game management. Charles Scribners Sons. N.Y., 1933.
Marquiss M., Newton I. - British Birds, 1982, 75, p. 243-260.
Marcström V. - Svensk Jakt, 1982, 120, p. 102-105.
Marcström V., Kenward R.E. - Viltrevy, 1981, 12, p. 3-35.
Marcström V., Widén P. - Svensk Jakt, 1977, 115, p. 98-101.
Mech C.D. - J. Wildl. Mgmt, 1967, 31 (3), p. 492-496.
Mech C.D. The wolf. Nat. Hist. Press. N.Y., 1970.
Mueller H.C. - Auk, 1974, 91, p. 705-721.
Mueller H.C., Berger D.D., Allez G. - Auk, 1977, 94, p. 652-663.
Murton R.K. The Woodpigeon. L.: Collins New Naturalist Series, 1965a.
Murton R.K., Isaacson A.J., Westwood N.J. - J. appl. Ecol., 1966, 3, p. 55-96.
Murton R.K., Isaacson A.J., Westwood N.J. - J. Zool. Lond., 1971, 165, p.53-84.
Murton R.K., Westwood N.J., Isaacson A.J. - Ibis, 1964, 106, p. 482-507.
Newton I. - Ardea, 1980, 68, p. 11-30.
Newton I., Marquiss M. - J. Zool. Lond., 1982, 197, p. 221-240.
Opdam P., Thissen J., Verschuren P., Müskens G. - J. Orn., 1977, 118, p.35-51.
Pearson O.P. - J. Anim. Ecol., 1966, 35, p. 217-233.
Perrins C.M., Geer T.A. - Ardea, 1980, 68, p. 133-142.
Phelan F.J.S., Robertson R.J. - Can. J. Zool., 1978, 56, p. 2565-2572.
Pielowski Z. - Ekologia Polska Ser A, 1961, 9, p. 183-194.
Pitelka F.A., Tomich P.Q., Treichel G.W. - Ecol. Monogr., 1955, 25, p.85-117.
Potts G.R. - Adv. Ecol. Res., 1980, 11, p. 1-79.
Powell R.A. - Am. Nat., 1980, 115, p. 567-579.
Schnell J.H. - J. Wildl. Manage., 1968, 32, p. 698-711.
Schnurre O. - Mitt. Ver. sächs. Ornith., 1935, 4, p. 211-225.
Schnurre O. - Z. Jagdwissenschaft, 1965, 11, p. 121-135.
Siewert H. - J. Orn., 1933, 81, p. 44-94.
Southern H.N. - J. Zool. Lond., 1970, 162 (2), p. 197-285.
Sulkava S. - Aquilo, Ser. Zool., 1964, 3, p. 1-103.
Thissen J., Müskens G., Opdam P. - In: Understanding the Goshawk / Eds.
    R.E.Kenward, I.Lindsay. Int. Assoc. Falconry Cons., 1981, p. 28-43.
Uttendörfer O. Neue Ergebnisse über die Ernährung der Greifvögel und Eulen.
    Stuttgart: Eugen Ulmer, 1952.
Von Bittera J. - Aquila, 1915, 22, p. 216-218.
Widén P. - In: Understanding the Goshawk / Eds. R.E.Kenward, I.Lindsay. Int.
    Ass. Falconry Cons. Birds of Prey, 1981, p. 114-120.
Wikman M. - Viltrapport, 1977, 5, p. 59-72.
Wikman M., Lindén H. - In: Understanding the Goshawk / Eds. R.E.Kenward,
    I.Lindsay. Int. Assoc. Falconry Cons. Birds of Prey, 1981, p. 105-113.
Ziesemer F. - In: Understanding the Goshawk / Eds. R.E.Kenward, I.Lindsay.
    Int. Ass. Falconry Cons. Birds of Prey, 1981, p. 144-151.
Ziesemer F. Untersuchungen zur Lebensweise von Habicht und Mäusebussard und
    zu deren Bedeutung für einige Niederwildarten. Unpublished research
    report, Staatliche Vogelschutzwarte Schleswig-Holstein. Berlin, 1982.

# THE ROLE OF PREDATORY BIRDS IN THE ECOSYSTEMS OF THE BYELORUSSIAN LAKE REGION

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The study of the role of predatory birds in ecosystems is of great scientific and practical interest in developing optimal methods of managing animal populations and ecosystems as a whole.

The present communication is based on data on predatory bird ecology in Northern Byelorussia obtained in 1962-1982 (Dorofeev, 1966; Dorofeev, Ivanovsky, 1980; Ivanovsky, Umanskaya, 1981 and others). The total census route was 1450 km, and the aircraft census covered an area of 28 000 $km^2$. To reveal territorial relationships of predatory birds, their nesting ranges were mapped annually at biological stations. Over 4 000 individuals of vertebrates were identified in pellets and prey remnants. Prey censuses were made, and selective morphological and parasitological analysis of populations of certain species was performed. The methods applied are similar to those described elsewhere (Golodushko, 1961; Galushin, 1962, 1971; März, 1972).

The study area (40 1000 $km^2$) is in the mid-course of the Zapadnaya Dvina river. Forestland accounts for a large proportion of the territory; there is a dense network of rivers (25 km per 100 $km^2$ of territory), there are many lakes (up to 12%) and bogs (10.6%). Farming lands constitute 50% of total area.

Of the 18 _Falconiformes_ species nesting in the Lake Region, 6 are common (Goshawk, Sparrow-Hawk, Common Buzzard, Lesser Spotted Eagle, March-Harrier Hobby) 5 are small numbered (Honey Buzzard, Black Kite, Montagu's Harrier, Hen Harrier, Kestrel), 7 rare or very rare (Osprey, White-Tailed Eagle, Spotted Eagle, Golden Eagle, Short-Toed Eagle, Merlin, Peregrine Falcon).

Territorial and trophic relationships of birds of prey are largely determined by the complexity of the forestland-lake-marshland landscape and the degree of its modification. Anthropogenic succession of ecosystems results in the reduction of the area and modification of the structure of the nesting habitats of the majority of birds, which, in its turn, determined the nature of inter- and itraspecific relations associated with nesting. In high bogs, which are least modified by man, the stability and diversity of habitats excludes, almost completely, interspecies competition for nesting sites. 90% of the Merlins nesting there occupy the same nesting ranges every year, whereas in a man-modified landscape—only 40%. The nesting territory of three Merlin couples in the high bog Obol averaged 1.200 ha, while that of 2 couples in a cultural landscape was 1.800 and 2.000 ha respectively. In high bogs, it is Merlin alone that uses the nests of the Hooded Crow, whereas in a cultural landscape, its competitors are the Kestrel, Hobby and Long-Eared Owl.

The degree of habitat transformation is determined to a greater extent by the nature of tropich relationships. The diet of Golden Eagles nesting in a mildly-modified landscape (Obol Biological Station) includes 49 species, while that of the couples nesting in a highly-modified landscape (Sokolische

T a b l e  1. Diet spectra and level of impact (f) on prey populations in different pair couples of Golden Eagles (Biological Stations Obol and Sokolische, 1976-1982)

| Prey species | Obol 180 km$^2$, including marsh lands-50, forestlands-100, farming lands-30 | | Sokolische 200 km$^2$, including marsh lands-18, forestlands-40, farming lands-142 | |
|---|---|---|---|---|
| | n% (n = 294) | f | n% (n = 117) | f |
| Anas platyrhynchos | 13.9 | 4.5 | 7.7 | 6.0 |
| Lagopus lagopus | 2.0 | 2.9 | 1.7 | 3.1 |
| Lyrurus tetrix | 29.3 | 4.2 | 22.2 | 5.1 |
| Tetrao urogallus | 8.2 | 1.8 | 11.1 | 2.0 |
| Numenius arquatus | 5.8 | 3.1 | 0.9 | 3.8 |
| N. phaeopus | 0.7 | 0.4 | 4.3 | 0.6 |
| Aves | 78.6 | - | 50.6 | - |
| Lepus | 13.3 | - | 37.6 | - |
| Carnivora | 2.4 | - | 8.5 | - |
| Carrion | 0.3 | - | 1.7 | - |
| Mammalia | 21.4 | - | 49.4 | - |

Total: Obol - 49 species
       Sokolische - 19 species

Biological Station)-only 19. The latters' prey is characterized by a considerable decline of the proportion of birds along with an equally increased share of mammals (Hares, Carnivores). An estimate of the impact of Golden Eagle on the populations of some of its prey shows than in greatly-modified ecosystems the predator-prey relationships are more strained (Table 1).

Characteristically, the maximal impacts of birds of prey on some prey populations were recorded there for individual couples of birds with a narrow diet range. For instance, in a Goshawk couple 60,0% of prey was accounted for by Rock-Doves (impact level 15.0), and in another - 80.0% by Rooks (impact level 8.0). 64% of prey of a couple of Common Buzzards are juvenile Blackbirds, Fieldfares and Song Thrushes (impact level 11.0-14.0).

The total impact on the populations of some bird species in undisturbed ecosystems does not exceed 6.7% (Table 2). The maximal pressure of predators is suffered by some common birds (Mallard, Black Grouse, Curlew, Golden Plover, Meadow Pipit) which make the bulk of their diet, and also some rare birds (Black-Throated Diver, Willow Grouse, Grey Shrive) killing in large numbers species which populate high bogs (Lapwihg), Redshank, as well as species that are not characteristic of the above habitat (Cuckoo), birds of prey promote the maintenance of a stable ornithocenosis in the ecosystem concerned. Rare species affect the populations of some prey within the nesting range to a greater extent compared with common species. The impact of a couple of golden eagles on populations of Mallard, Black Grouse, Willow

T a b l e  2. The impact of the Golden Eagle, Goshawk and Merlin on populations of some birds (Biological Station Obol, 180 km$^2$, 1976-1982)

| Prey | Impact (%) | | | |
|---|---|---|---|---|
| | Aguila chrysaetos (1 couple) | Accipiter gentilis (5 couples) | Falco columbarius (3 couples) | Total |
| Gavia arctica* | 4.4 | - | - | 4.4 |
| Anas platyrhynchos | 4.5 | 0.6 | - | 5.1 |
| A.crecca | 1.4 | 1.1 | - | 2.5 |
| Lagopus lagopus* | 2.9 | 1.6 | 0.1 | 4.6 |
| Lyrurus tetrix | 4.2 | 2.5 | - | 6.7 |
| Tetrao urogallus | 1.8 | 0.2 | - | 2.0 |
| Grus grus | 2.5 | - | - | 2.5 |
| Pluvialis apricaria* | - | - | 5.0 | 5.0 |
| Vanellus vanellus* | - | - | 5.1 | 5.1 |
| Tringa glareola* | - | - | 1.0 | 1.0 |
| T.totanus* | 0.07 | - | 5.2 | 5.27 |
| Gallinago gallinago | - | 0.1 | 0.9 | 1.0 |
| Numenius arquatus* | 3.1 | 1.2 | - | 4.3 |
| N.phaeopus* | 0.4 | 0.6 | - | 1.0 |
| Limosa limosa | 0.3 | - | - | 0.3 |
| Cuculus canorus | 0.8 | 0.9 | 4.0 | 5.7 |
| Alauda arvensis* | - | - | 2.0 | 2.0 |
| Corvus corax | 2.6 | 1.5 | - | 4.1 |
| Corvus cornix | 0.3 | 4.1 | - | 4.4 |
| Anthus trivialis* | - | - | 1.0 | 1.0 |
| A.pratensis* | - | - | 4.0 | 4.0 |
| Lanius excubitor* | 0.3 | - | 5.3 | 5.6 |

*  Impact is only calculated for the high bog area (5,015 ha).

Grouse and Curlew exceeds that of 5 couples of Goshawks. On the whole in the Lake Region, 20 couples of Golden Eagles take, during the nesting period (75 days) 1.7 times as many Curlews, 2.4 times as many Willow Grouse, 3.3 as many Mallaras, and by a factor of 5.6 less capercailzies compared with 440 couples of Goshawks take during 43-45 days.

Qualitative analysis of prey remains is indicative of a high selectiveness of Falconiformes in relation to a particular category of individuals within a definite species. In fact, of the 170 Black Grouses and 50 Capercaillies killed by the Golden Eagle whose bone remains were analyzed, individuals with old fractures and other pathological changes of bones acounted for about 9.8%, while among the 70 Black Grouse and 20 Capercaillies taken by hunters - only 1.0%. In the kill of Goshawks, Jay individuals with various defects, accounted for 33.3% (9 out of 27) while in a sample - 5.0% (2 out of 40).

In the kill of a couple of Goshawks that specialized in hunting Rock-Doves, individuals with deviant colouration constituted 40.0%, while in flocks

in the countryside settlement where this couple hunted - only 5.0. In Vi-
tebsk, where Hawks do not hunt during the nesting period, the value in ques-
tion was 14.7%. In the kill of 5 couples of Kestrel and 3 couples of Long-
Eared owls, the incidence of occideiasis and helminthiases among common vo-
les was 4.6 times as frequent (23 individuals out of 160) as in control
samples (5 individuals out of 160).

In the course of conjugated evolution of both elements of the predator -
prey system, the trophic relations are the major factor limiting the number
of predatory birds (Newton, 1980). An important factor of stabilizing se-
lection, predatory birds are conductive to equilibrium in the ecosystem and
to an optimal structure of prey populations.

SUMMARY

The study of predatory birds in the ecosystems of Northern Byelorussia
(1962-1982) has revealed that in undisturbed ecosystems their overall im-
pact on prey populations does not exceed 6.7%. In highly-modified ecosystems,
this value may attain 8.0-15.0% in couples with a narrow feeding speciali-
zation.

Populations of rare predatory birds affect those of most prey to a 1.7-
5.6 lesser extent than common birds. A marked selectiveness of on the part
of predators to morphologically or physiologically defective prey has been
revealed. In disturbed ecosystems, the predator- prey relations are more
strained.

R e f e r e n c e s

Dorofeev A.M. - In: Proc. of the VIth Baltic Ornithological Conference.
    Vilnius, 1966, p. 58-59
Dorofeev A.M., Ivanovsky V.V. - Westnik zoologii, 1980, N 5, p. 62-67 (in
    Russian).
Galushin V.M. - In: Materials of fauna and ecology of animals. Transactions
    of the Moscow Pedagogical Institute named after V.I.Lenin. Moscow, 1962,
    N 186, p. 115-151
Galushin V.M. - In: Transactions of the Oka State Reserve. Moscow, 1971, p.3
    132
Golodushko B.Z. - In: Fauna and ecology of terrestrial vertebrates of
    Byelorussia. Minsk, 1961, p. 98-111
Ivanovsky V.V., Umanskaya A.S. - Vest. zool., 1981, N 4, p. 61-65

März R. Gewöll- und Rupfungskunde. B.,1972, S. 1-287.
Newton J. - Ardea, 1980, 18, N 1-4, p. 11-30.

# MANAGEMENT ZUR ANHEBUNG DES GREIFVOGELBESTANDES

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Management ist heutzutage ein viel benutzter Ausdruck, der seinen Eingang aus dem Amerikanischen auch in die Terminologie der Biologie bzw. Ökologie gefunden hat. Ursprünglich kommt das Wort jedoch aus dem Italienischen. Die wörtliche Übersetzung lautet etwa "handhaben". Unter Populationsmanagement möchte ich hier im weitesten Sinne die bewusste Beeinflussung der Greifvögel-bestände durch den Menschen verstehen. Jahrhundertelang bestand diese fast asschliesslich in der Reduzierung durch Abschuss, Fang, Zerstörung der Brut-stätten usw. Erst mit dem Wandel des menschlichen Denkens und dem rapiden Rückgang der Greifvögel begann sich auch mehr und mehr der Greifvogelschutz durchzusetzen. Unter Management wird daher heutzutage in erster Linie die positive Beeinflussung der Bestände verstanden. Geht man davon aus, da seit Beginn des vorigen Jahrhunderts in Europa ein Zusammenschmelzen der Zahl der Greifvögel auf etwa 1% stattgefunden hat (Voous in Bijleveld, 1974), so steht die Notwendigkeit einer Beeinflussung der Populationen durch moderne Manage-menttechniken ausser Frage. Ein vollständiger gesetzlicher Schutz sämtlicher Greifvogelarten in allen Ländern der Erde ist dazu eine selbstverständliche Voraussetzung, wie dies u.a. auch in Resolution 2 der Weltkonferenz für Greifvögel 1975 in Wien gefordert wurde. Für eine Regulierung von Greifvögeln im Sinne der Reduzierung, wie sie gelegentlich noch immer von einigen Jägern gefordert wird, vermag ich nicht die geringste Berechtigung zu sehen. Für Ausführungen über die Gründe einer Ablehnung der heutigen Bejagung von Greif-vögeln ist hier nicht der Raum, auch haben zahlreiche Authoren (z.B.Sothmann, 1978) hierzu ausführlich Stellung genommen. Glücklicherweise sind inzwischen in Europa in den meisten Ländern alle Greifvogelarten ganzjährig geschützt.

Vor jedem praktischen Versuch des Populationsmanagements von Greifvögeln muss die Beantwortung der Frage stehen, wodurch ihre Zahl begrenzt wird bzw. welches die limitierenden Faktoren sind. Es wäre vollkommen sinnlos, die In-dividuenzahl in einem Habitat erhöhen zu wollen, in dem die Tragfähigkeit desselben schon erreicht ist.

Drei Hauptgründe sind für den weltweiten Rückgang vieler Greifvogelarten verantwortlich: Habitatveränderungen, menschliche Verfolgung und Kontamina-tion mit toxischen Chemikalien. Die Tragfähigkeit eines gegebenen Lebensrau-mes wird unter Ausschluss direkter menschlicher Einwirkung normalerweise haupt-angebot. Nur unter Berückeichtigung dieser Grundtatsachen ist die Anwendung eines Greifvogelmanagements sinnvoll.

Viele moderne Greifvogelmanagementtechniken im engeren Sinne - man könnte sie auch aktive Managementtechniken nennen - wurden erst in den letzten 10-15 Jahren entwickelt. Sie greifen zum Teil recht drastisch unmittelbar in das Leben der Tiere ein. Wohl aus diesem Grunde werden sie teilweise noch von einigen konservativ eingestellten Vogelschützern kritisiert. Eine gewisse Skepsis ist in Bezug auf manche Techniken sicherlich vorerst auch noch ange-bracht. Andererseits sollte man dabei nicht vergessen, dass in einigen Fällen hierin die vielleicht letzte Chance für eine Art bestehen kann. Jahrzehntelang hat man in herkömmlicher Weise z.B. vergeblich versuch:, den weiteren Rück-gang des Kalifornischen Kondors zu verhindern. Wird jetzt der Versuch, die

Vögel in Gefangenschaft zu züchten, zu spät kommen? Ein Jahrzehnt lang benötigte man für den notwendigen Kampf gegen DDT in den U.S.A. Während dieser Zeit wurde der Wanderfalke nur in üblicher konservativer Weise geschützt und starb im Osten des Kontinents aus. Jetzt nachträglich wird diese Verfahrensweise von einigen bedauert. Auch der Seeadler stand in Mitteleuropa um die Jahrhundertwende unmittelbar vor dem Aussterben. In Mecklenburg, seinem Verbreitungszentrum, konnte man die Paare an den Fingern einer Hand zählen. Gerade noch rechtzeitig liess dann der Jagddruck nach und die Populationsgrösse nahm wieder einige Zeit lang zu. Nicht mehr geschafft hat es in Mitteleuropa der Bartgeier, und es bleibt abzuwarten, ob die Bemühungen um seine Wiedereinbürgerung in den Alpen Erfolg haben werden.

Man muss sich unbedingt vor Augen halten, dass die weiter unter beschriebenen Managementmethoden nicht etwa in Konkurrenz zu den klassischen Schutzmassnahmen, wie juristischer Schutz vor direkter Verfolgung und Erhaltung der Habitate (passives Management), stehen. Dies sind vielmehr nach wie vor die Grundvoraussetzungen für das Überleben einer Population in freier Wildbahn, andererseits aber oft nicht allein ausreichend oder manchmal nicht rechzeitig erreichbar. In unserer sich rasch verändernden Welt, in der es offenbar nicht gelingt, das Hauptproblem der rapide zunehmenden menschlichen Population und all ihrer Folgen in den Griff zu bekommen, scheint für manche Greifvogelarten zumindest vorübergehend die vielleicht einzigs Chance in dem zu bestehen, was Zimmerman (1975) mit dem Begriff "klinische Ornithologie" umrissen hat.

## I. Verbesserung des Nistplatzangebotes und der Nistplatzsicherheit

Greifvögel gehören zu den wenigen Vögeln, deren Zahl und Bruterfolg in einigen Gegenden deutlich durch das Nistplatzangebot limitiert wird (Newton, 1979: 81). Hierin besteht eine bisher kaum genutzte, aber in ihrer Bedeutung kaum zu überschätzende Möglichkeit, die Brutdichte und selbst Verbreitung vieler Arten positiv zu beeinflussen. Ein Hindernis dürfte nicht zuletzt in der etwas romantischen Vorstellung vieler bestehen, Greifvögel müssten an wilden und abgelegenen Plätzen nisten. Ein Steinadlerhorst gehört beispielsweise sicherlich nach der Ansicht selbst vieler Kenner in eine steile Felswand und nicht auf einen Hochspannungsmast in der Kultursteppe. Und doch fand man in den Vereinigten Staaten allein in einem kleinen Teil des Staates Idaho 32 Horste von Greifvögeln auf Hochspannungsmasten, davon mindestens 17 des Steinadlers. Durch entsprechende Konstruktionen liessen sich diese Masten so gestalten, dass die Vögel darauf sicherer als an natürlichen Plätzen brüten konnten. Vorher waren diese Stellen überhaupt nicht besiedelbar gewesen. In Europa könnten andere grosse baumbrütende Arten wie Seeadler, Kaiseradler und Mönchsgeier, denen durch die systematische Abholzung der Altholzbestände vollständig ihre Brutbiotope entzogen zu werden drohen, auf diese Weise vielleicht gerettet werden. Ausser der Horstplattform müsste wohl in manchen Fällen der Horstbaum in Form eines einfachen Holzmasten ersetzt werden. Da der Umgewöhnungsprozess an derartige Horstplätze nur sehr allmählich vonstatten gehen dürfte, müsste hier sehr langfristig experimentiert und geplant werden. Da diese Vorstellung auch in Europa nicht utopisch ist, beweisen die inzwischen fast ausschliesslich auf Masten horstenden Fischadler an der Müritz in Mecklenburg. Aber auch Habichtsadler Hieraaetus fasciatus und Spanischer Kaiseradler Aquila heliaca adalberti haben bereits auf Hochspannungsmasten gebrütet.

## I.a. Bruthilfe durch Nistkästen

Bereits 1895 wurde auf die Möglichkeit der Anbringung von Nistkästen für Turmfalken hingewiesen und vom erfolgreichen Brüten darin berichtet (Piechocki, 1970). Von Schmidt (1948) erschien eine ausführliche Arbeit über die Bruthilfe mit Hinweisen zum Bau von Brutkästen für den Turmfalken. Das wohl beste Beispiel in Europa, wie gross der Effekt des zur Verfügungstellens geeigneter Nistplätze unter bestimmten Bedingungen sein kann, lieferte Cavé 1959 betrug die Zahl der Paare in seinem Untersuchungsgebiet 20, davon 11 in Nistkästen. Ein Jahr später, nachdem 246 Kästen angebracht worden waren, wurden auf der gleichen Fläche 109 Paare gefunden.

## I.b. Kunsthorste für Baumbrüter

Der Greifvogelbestand in Mitteleuropa wird normalerweise eher durch das Nahrungsangebot als durch Mangel an Nistgelegenheiten begrenzt. Deshalb sollte man zunächst nicht erwarten, dass sich der Greifvogelbestand eines Gebietes durch das Anbringen von Kunsthorsten merklich heben lässt, denn in der Regel stehen jedem Brutpaar mehrere fertige Horste in seinem Brutrevier zur Verfügung.

Jedoch gibt hauptsächlich ein Umstand dazu Anlass, bestimmten Arten Kunsthorste anzubieten: Der bevorstehende Abtrieb eines grossen Teils der noch verbliebenen Altholzreste in einigen Teilen Mitteleuropas, in denen bisher viele Greifvögel zum Teil dicht gedrängt brüten, wofür sich viele Beispiele nennen lassen. Besonders See- und Fischadler, die über hundertjährige Bestände bevorzugen, sind am stärksten vom Mangel an Brutgehölzen betroffen. Zum anderen könnten viele Lebensräume für manche Arten neu erschlossen werden, würde es gelingen, sie in grösserem Umfang zum Brüten auf künstlichen Plätzen wie z.B. Hochspannungsmasten zu veranlassen.

In grösserer Zahl wurden in Europa Kunsthorste bisher nur in Schweden (Berggren, 1975) und Finnland (Saurola, 1978) errichtet. In Nord-Schweden wurden die Horste ausser von Bartkauz und Habichtskauz vom Mäusebussard, Raufu - bussard und Habicht angenommen. Helander (1975) gelang es in drei Fällen, Seeadler durch Anbieten von Kunsthorsten zum Brüten an ruhigeren Stellen zu bringen.

In Finnland wurden für den Fischadler über 200 Kunsthorste und weitere 200 Kunsthorste für andere Greifvögel errichtet. 1977 beispielsweise waren in einem Gebiet 60 Fischadlerhorste beflogen, davon nur 21 in natürlichen Horsten. Auch Mäusebussarde haben die Kunsthorste gut angenommen. Auf einer Probefläche fanden 26 von 50 Bruten in Kunsthorsten statt. Die Bruterfolge beider Gruppen waren etwa gleichgross. In einigen Fällen wurden die Kunsthorste auch von Habicht, Sperber, Baumfalke und Wespenbussard benutzt.

## I.c. Künstliche Nischen und Nistkästen für Felsbrüter

Diese Managementtechnik kam bisher besonders systematisch in Kanada zur Anwendung (Fyfe, Armbruster, 1977). Im Rahmen eines experimentellen Nistplatzverbesserungsprogramms wurden seit 1970 über 200 Horstnischen für Prairiefalken geschaffen oder verbessert. Mit der Hand oder einer Schaufel wurden Löcher von 30 x 60 x 30 c Grösse hergestellt, die zu etwa ein Viertel in der Folge benutzt wurden.

Auch in Europa werden dem Wanderfalken zusätzliche sichere Nistplätze erfolgreich angeboten. Es werden in glatte und mardersichere Felswände Nischen hineingesprengt oder aus Buntsandsteinplatten hergestellte Nistkästen an glatter Wandpartie aufgehängt. Diese Kästen wiegen 200 kg und sollen 50 Jahre halten. Zu ihrer Befestigung sind acht Kletterer notwendig. Trotzdem ist die Aufhängung dieser Nistkästen nur halb so arbeitsaufwändig wie das Heraussprengen von Nistnischen, was z.B. in steinschlaggefährdeten Sandsteinbrüchen auch kaum möglich ist.

## I.d. Künstliche Horstplattformen auf Masten, Gebäuden usw

In baumlosen Trassen dienen die Masten von Hochspannungsleitungen dem Mäusebussard und anderen Vogelarten als Ansitz und Schlafplatz. Zum Brüten werden sie am häufigsten in Mitteleuropa bisher vom Fischadler benutzt. Im Müritzgebiet in Mecklenburg horsteten bereits 1960 14 von 20 Paaren auf Hochspannungsmasten. Es wurden bisher etwa 25-30 eiserne Plattformen auf den Masten montiert, nicht nur aus Naturschutzgründen, sondern auch um Störungen an den Leitungen zu vermeiden. In der Schorfheide (nördliche Mark Brandenburg) sind mir hingegen keine Horste auf Leitungsmasten bekannt. Tradition spielt also offenbar auch eine Rolle.

Diese Technik verdient unbedingt, dass man sich ihr auch in anderen Ländern eingehender widmet. Durch entsprechende Gestaltung der Masten liesse sich sicherlich auch hier erreichen, dass weitere Arten in grösserer Zahl hier sichere Nistplätze finden. Die Forschungsarbeit von Nelson & Nelson (1977) in den Vereinigten Staaten kann auf diesem Gebiet als richtungsweisend gelten.

## I.e. Sicherung von Horsten gegen Absturz

Die Horste mancher Arten sind durch ihren Standort und ihre Bauweise sehr absturzgefährdet. Die proportional grössten Verluste erleidet in Europa wohl der äusserst seltene Kaiseradler durch die Instabilität seiner den Bäumen "aufgesetzten" Horstkonstruktion. Von 20 in der Ostslowakei gefundenen Horsten waren bis 1978 mindestens 9 heruntergefallen, während 3 weitere Horstbäume gefällt worden waren (Svehlik, Meyburg, 1979). Ausser durch Anbieten fester künstlicher Horste kann diesem Vogel durch frühzeitiges Befestigen absturzgefährdeter Nester sehr wirksam geholfen werden.

## I.f. Sicherung gegen Störungen und Zerstörungen durch Menschen und tierische Feinde

Auf diesem Gebiet hat man in den letzten 10-15 Jahren mancherorts ausserordentliche Fortschritte erzielen könne. Es haben sich Arbeitsgruppen gebildet, die mit grosser Zähigkeit gefährdete Brutplätze wochen- und monatelang bewachen, wobei sie sich zum Teil hochwertiger Technik bedienen. So wird beispielsweise der Zugang zu den wenigen Seeadlerhorsten in der Bundesrepublik Deutschland in einem Umkreis von ca. 500 m gesperrt. Die Horstbäume werden mit Kletterhindernissen, wie Stachelringe, und mit Hilfe von Mikrofonen gesichert. 60-120 freiwillige Helfer werden jährlich für die Bewachung eingesetzt. Auf ähnliche Weise werden alljährlich beispielsweise die Horste von Fischadlern in Schottland und auf Korsika und die von Wanderfalken in Deutschland und Frankreich bewacht.

Die einer Untersuchung an in der Bundesrepublik Deutschland brütenden Wanderfalken wurde in 7 von 40 kontrollierten Horsten das Auftreten der Zeckenart

_Ixodes arboricola_ nachgewiesen. Die Sterblichkeit der mit Zecken befallenen Nestlinge betrug 74%. Zur Bekämpfung der an Wanderfalkennestlingen angesaugten Zecken wurde mit gutem Erfolg eine 1% ige wässrige Suspension von Antorgen verwandt. Die Behandlung der Horste erfolgte mit einer 3% igen Suspension desselben Mittels. Antorgan ist ein Insektizid und Akarizid auf der Basis eines Phosphorsäureesters mit Langzeitwirkung, das bei Haustieren einschliesslich Hausgeflügel angewendet wird. Es wird empfohlen, mit Zecken befallene Horste jährlich mindestens dreimal gründlich auszusprühen: Einmal kurz nach dem Ausfliegen der Jungvögel im Sommer, dann wieder im Frühjahr kurz vor Brutbeginn und ein weiteres Mal beim Beringen der Jungvögel (Schilling et al., 1981).

## I.g. Andere Manipulationen zur Verhinderung von Brutverlusten

1974 wurden forstliche Arbeiten in der Nähe eines Kaiseradlerhorstes in den ostslowakischen Karpaten durchgeführt, die dazu führten, dass das Weibchen nicht mehr regelmässig die noch unbefiederten Jungen hudern konnte. Da es nicht möglich war, diese Arbeiten sofort zu stoppen und andererseits der baldige Tod der beiden Jungen wegen des kalten und regnerischen Wetters zu befürchten war, wurden diese aus dem Nest genommen und dafür zwei junge Mäusebussarde in den Adlerhorst gesetzt. Diese wurden auch angenommen und von den Adlern gefüttert. Da die jungen Bussarde schon vollständig befiedert waren, machte es ihnen nichts aus, dass sie nicht gehudert werden konnten. Bei den Adlern hingegen blieb die Bindung an den Horst bestehen. Als die Forstarbeiten abgeschlossen waren, wurden die Jungen wieder ausgetauscht. Beide jungen Adler wurden daraufhin problemlos weiter aufgezogen.

In ähnlicher Weise gelang es auch bei anderen Greifvogelarten (z.B. Seeadler, Habicht, Sperber) gefährdete oder sogar bereits aufgegebene Bruten zu retten.

## II. Erhöhung der Reproduktionsrate

Die Fortpflanzung ist neben der Sterblichkeit der Hauptfaktor, der für die Populationsgrösse einer Art verantwortlich ist. Es ist daher nicht verwunderlich, dass viele Managementtechniken hier ihren Ansatzpunkt haben. Während bei den im vorigen Abschnitt über die Verbesserung des Nistplatzangebotes und der Nistplatzsicherheit beschriebenen Methoden noch relativ passiv versucht wird, die Fortpflanzungsrate zu erhöhen, kommen wir jetzt zu einigen Techniken, die sehr direkt in das Leben freilebender Tiere eingreifen. Verantwortungsbewusstsein und Erfahrung ist daher hierbei in besonderem Masse zu fordern.

Voraussetzung für diese Methoden sind ferner die volle Ausschöpfung des passiven oder konventionellen Managements sowie - sofern notwending - auch die Anwendung der im vorigen Abschnitt (I.) genannten Schutzmassnahmen; denn es ist beispielsweise natürlich nur sinnvoll, den Kainismus zu verhindern, wenn auch das Überleben der gesamten Brut soweit gesichert ist. ·

## II.a. Induzierung von Zweitgelegen

Seit der frühen Zeit der Oologen des vorigen und Beginn dieses Jahrhunderts wissen wir, dass manche Greifvogelarten häufig oder teilweise sogar regelmässig ein Zweitgelege produzieren, wenn sie ihr erstes kurz nach der Eiablage verlieren (Nethersole-Thompson, 1931; Wittenberg, 1964). Diese

Tatsache versuchte man besonders beim Wanderfalken und Fischadler zur Steigerung der Reproduktion zu nutzen.

In 9 Fällen entnahmen Fyfe et al. (1978) in den letzten Jahren in Kanada frische Wanderfalkengelege. Zwei Drittel der Paare zeitigten eine Zweitbrut. Bis auf einen Fall enthielten die Nachgelege ein Ei weniger als die Erstbruten. Diese Rate stimmt gut mit den frühen Angaben von Nethersole-Thompson (1931) aus England überein. Nach Wittenberg (1964) zeitigten norddeutsche Baumbrüter häufig, teilweise sogar regelmässig, ein Nachgelege und manchmal auch ein zweites. Das 1. Nachgelege war in Norddeutschland durchschnittlich mindestens ebenso stark wie das Normalgelege. Bei deutschen Felsenbrütern scheinen unter gleichen Bedingungen Nachgelege selten zu sein, vielleicht aus Mangel an Ersatz-Horststellen. Das Ergebnis entsprechender Experimente in Ostfrankreich, kombiniert mit Adoption in Gefangenschaft, wird von Monneret (1978) wie folgt angegeben: Bei 10 Paaren wurden 17 Erstgelege entfernt, die alle ersetzt wurden. Die Erstgelege ergaben 17 Küken, von denen 10 flügge wurden. 20 Nestlinge aus den Ersatzbruten wurden flügge, zusammen also 30. Unter Ausschluss von 2 Paaren mit normaler Fortpflanzungsrate ergab dies 16 Junge für 8 fast "sterile" Paare, die in vier vorangegangenen Jahren zusammen nur 10 Jungvögel hochgebracht hatten.

Auch aus anderen Angaben ergibt sich, da die Weibchen offenbar bei der Produktion der Erstgelege einen Teil ihrer Pestizide verlieren und dadurch die Eischalendicke des Nachgeleges grösser und die Wahrscheinlichkeit abnormen Verhaltens geringer wird. Gleiches wurde auch beim Fischadler in den U.S.A. gefunden (Kennedy, 1977). Auch hier war der Schlüpferfolg der Nachgelege deutlich besser als der der Erstbruten.

Während diese Technik der Erhöhung der Reproduktionsrate bei Wildvögeln zum Teil umstritten ist, wird sie in der Zucht inzwischen regelmässig mit grossem Erfolg angewandt.

## II.b. Ei- und Nestlingsverfrachtung

Durch die Anwendung gewisser Pestizide kam es bekanntlich zu einem Rückgang der Reproduktionsrate nicht weniger Greifvogelarten. Dabei sind oft nicht alle Populationen einer Art gleich stark betroffen. Dadurch ergibt sich die Möglichkeit, den Rückgang stark kontaminierter Populationen durch den Austausch der Eier und Jangen der mit in weniger betroffenen Gebieten lebenden Paare zu verhindern.

In einem entsprechenden Experiment verfrachtete Spitzer (1978) 1968-1970 53 Eier bzw. Nestlinge des Fischadlers aus Horsten in Maryland (U.S.A.) in Nester in Connecticut. 45 der Jungadler flogen aus. Diese Rate von 85% entsprach der in Maryland. Mindestens 7 dieser Vögel kehrten in den darauffolgenden Jahren nach Connecticut zurück, und 3 von ihnen pflanzten sich dort erfolgreich fort.

Wenn die Reproduktionsrate der jenigen Paare nicht vermindert werden soll, aus deren Horsten Junge oder Eier entfernt werden, so muss es hier eine natürliche Nestlingssterblichkeit geben oder es müssen regelmässig Nachgelege produziert werden. Ein typisches Beispiel ist der Spanische Kaiseradler Aquila (heliaca) adalberti. Zwischen 1971 und 1979 kontrollierte ich 39 Bruten zur Schlupfzeit in Zentralspanien, wobei 10 mal 1, 4 mal 2, 14 mal 3 und 5 mal 4 Küken schlüpften, während in 6 weiteren Horsten die Gelege unbefruchtet

688

oder die Embryonen abgestorben waren. Zwar können bis zu 4 Junge aufgezogen werden, aber in der Regel kommen bei Bruten mit mehr als einem Küken die zuletztgeschlüpften während der ersten Lebenswochen um. Wie bei vielen Greifvogelarten legen die Nestlinge nämlich anfangs gross Unverträglichkeit an den Tag. Da sie infolge unterschiedlicher Schlüpftermine verschieden gross sind, fallen die jüngsten Nestinsassen in der Regel der Aggressivität ihres grössten Geschwisters zum Opfer.

Um den Verlust dieser Nestlinge zu verhindern, müssen sie aus dem Horst genommen und in andere Nester gesetzt werden, die ein unbefruchtetes Gelege oder nur ein etwa gleichgrosses Junges beinhalten, wo sie dann aufgezogen werden. Können keine derartigen Horste zum Einsetzen der Jungen gefunden werden, bleibt nur die Handaufzucht. Sobald die kritische Phase vorüber ist, können die Jungvögel vor dem Ausfliegen in den elterlichen Horst zurückgesetzt oder woanders ausgewildert werden.

Beim Spanischen Kaiseradler konnte gezeigt werden, dassauf diese Weise der Tod von 30% der geschlüpften Jungen verhindert und damit die Zahl der ausfliegenden Jungen um 43% erhöht werden kann (Meyburg, Garzon Heydt, 1973). Bei mindestens 27 Adlerarten der Erde sowie vielen anderen Greifvogelarten, die regelmässig mehr,als ein Ei legen, sterben zulstztgeschlüpfte Küken mehr oder weniger regelmässig.Dies eröffnet die Möglichkeit, die Portpflanzungsrate dieser Arten erheblich künstlich zu steigern oder junge Vögel für Zuchtzwecke zu gewinnen, ohne der Wildpopulation Schaden zuzufügen. Entsprechende positiv verlaufene Experimente wurden auch bei einer ganzen Reihe anderer Arten gemacht (Meyburg, 1978).

## II.c. Verhinderung des Kainismus

Eine Reihe von Greifvogel-, Kranich-, Tölpel-, Raubmöwen-, Pinguin- und Kakaduarten legen regelmässig zwei Eier, ziehen normalerweise,aber nur eines der geschlüpften Küken auf. Bei Adlern hat sich für diesen eigenartigen und interessanten Vorgang der Terminus "Kainismus" eingebürgert. Er ist der alttestamentarischen Geschichte vom Morde Kains und Abel entlehnt, denn der Tod des zweiten Jungen wird durch das ältere bedingt. Nahrungsmangel spielt in diesen Fällen keine Rolle, wie experimentelle Untersuchungen ergeben haben. Vom Kainismus unterscheiden wir den Fratrizid, bei dem der Tod der jüngeren Nestgeschwister eher durch Nahrungsmangel bedingt wird und die kleineren Nestinsassen bei reichlichem Nahrungsangebot überleben können. Der Übergang zwischen beiden Formen ist jedoch fliessend.

Bei einer Population des Schreiadlers Aquila pomarina in der Ostslowakei, bei der in 26 erfolgreichen Horsten 42 Küken geschlüpft waren, bedingte diese Ursache den Tod von 38% aller Nestlinge, Einerbruten mit eingerechnet. Durch die von Meyburg (1971, 1972, 1977, 1978a,b) beschriebenen Methoden lässt sich der Verlust des zweiten Jungadlers verhindern und dieser in seinem Horst zum Ausfliegen bringen. Dabei wird er entweder während der kritischen Phase der Nestlingszeit in Menschenobhut aufgezogen oder vorübergehend zur Adoption in den Horst anderer Arten (Mäusebussard, Schwarzmilan) gesetzt. Diese Techniken zur künstlichen Erhöhung der Fortpflanzungsrate wurden an 11 Horsten erfolgreich angewandt, erstmals 1968 bei zwei Paaren. Dabei war es lediglich die Aufgabe dieser Versuche, nachzuweisen, dass sich auf diesem Wege der Reproduk-

tionserfolg erhöhen lässt Um einen wirklichen Einfluss auf die Population-
sgrosse zu erreichen, müsste die Durchführung bei einer viel grösseren Zahl von
Bruten organisiert werden. Hätte man in der Slowakei in jedem Falle den Ka-
inismus verhindert, so wäre eine Steigerung der Reproduktionsrate um 81% er-
reicht worden (Svehlik, Meyburg, 1979). Verglichen etwa mit dem Aufwand, der
mit der Zucht eines jungen Greifvogels in Gefangenschaft und seiner Auswil-
derung verbunden ist, erscheint er bei dieser Technik recht gering, besonders
wenn sie mit Bestandsaufnahmen und brutbiologischen Studien gekoppelt wird.
In Anbetracht des starken Rückganges der Art in Mitteleuropa und anderen
Teilen ihres Verbreitungsgebietes ist eine Durchführung in grossem Rahmen
wünschenswert.

Auch bei anderen in Europa vorkommenden Arten, wie etwa dem Schelladler,
Steinadler, Seeadler, Zwergadler und Bartgeier kommt Kainismus vor. Die
Häufigkeit und die Ursachen wurden bisher noch nicht näher untersucht. Beim
Steinadler scheinen etwa 30-50% der zweitgeschlüpften Küken zu überleben.
Beim Bartgeier verschwinden die kleineren Geschwister normalerweise, die Grün-
de hierfür sind nach Gefangenschaftsbeobachtungen die gleichen wie beim
Schreiadler.

Bei Wiedereinbürgerungsversuchen dieser Arten sollte unbedingt auf diese
Todeskandidaten zurückgegriffen werden, sofern keine gezüchteten Vögel zur
Verfügung stehen. Andere Nestlinge auszuhorsten ist meines Erachtens nicht
zu verantworten.

### III. Reduktion der Mortalität der Wildpopulation und der Kontamination mit Pestiziden

### III.a. Behandlung von verletzten und geschwächten Greifvögeln und ihre Wiederfreilassung

Das zunehmende Interesse am Greifvogelschutz spiegelt sich mancherorts
auch in der Errichtung von sogenannten Greifvogelpflegestationen wider. Zwei
Gruppen von Greifvögeln werden in der Regel in solche Einrichtungen gebracht:
kranke oder verletzte Tiere und fälschlicherweise aufgenommene Jungvögel.

Da sich Greifvogelpopulationen in erster Linie in Abhängigkeit von ihren
Beutetieren regulieren, ist es nicht sinnvoll, jeden verletzten Vogel unter
allen Umständen am Leben zu erhalten. Greifvögel mit verheilten Knochenbrü-
chen, Muskel- oder Sehnenverletzungen beispielsweise haben in der Natur nur
geringe Überlebenschancen. Trotz bester Absichten besteht leider die Gefahr,
dass Greifvogelpflegestationen zu Menagerien entarten und sich dann kaum noch
von jenen Schaustellungen unterscheiden, die entschieden abzulehnen sind. Sta-
tionen, in denen Besucher Zutritt haben, sind nicht akzeptabel. Besonders
dort wächst nämlich die Versuchung, unnötigerweise Tiere zu halten, um eine
möglichst vollständige "Kollektion" präsentieren zu können. Die Pflege wird
dann zu eigennützigen Zwecken missbraucht und hat nur noch Alibifunktion. Die
Pflege von Greifvögeln sollte sich in erster Linie auf lebenstüchtige Tiere
beschränken, die nach einer gewissen Zeit wiederausgewildert werden können.
Jungvögel, die während der Ästlingsphase auf den Boden geraten sind, sollten
unbedingt in den eigenen, oder einen anderen Horst mit etwa gleichgrossen Jun-
gen zurückgesetzt werden.

## III.b. Zusätzliches Füttern im Winter und mit pestizidarmen Fleisch

Hierdurch versucht man seit einer Reihe von Jahren in verschiedenen Ländern die Populationen einiger Greifvogelarten, insbesondere von Geiern und Adlern, zu fördern. Umfangreiche, langjährige Fütterungsprogramme gibt es beispielsweise in Europa besonders für die Geier in den Pyrenäen und den Seeadler in Schweden und Mitteleuropa. Dazu werden ganze Tiere aus Schlachthäusern oder überfahrene Wildtiere oder Fleischabfälle in den Wintermonaten an geeigneten Stellen ausgelegt. Die bedrohteste Greifvogelart der Erde, die man unter anderem durch das Auslegen von Kadavern vor dem Aussterben zu bewahren versucht, ist der Kalifornische Kondor.

## III.c. Verhinderung von Stromunfällen und Kollisionen mit Leitungen

Stromunfälle an Hochspannungsmasten ereilen in erster Linie grosse Greifvogelarten (Adler und Geier), deren Flügelspannweite grösser als der Abstand zwischen zwei Drähten ist, so dass sie beim Landen und Abfliegen gleichzeitig zwei oder mehr Drähte berühren. Ganz überwiegend immature und subadulte (bis zu 98%) Vögel verunglücken. Ein genügender Abstand von mindestens 152 cm zwischen den einzelnen Drähten ist die wichtigste Voraussetzung zur Verhinderung derartiger Unfälle. Die umfangreichste Übersicht über diese Problematik und Lösungsmöglichkeiten haben Olendorf et al. (1981) zusammengestellt.

## IV. Aufstellung von Sitzkrücken auf Freiflächen

Durch diese Methode zur Schadnagereinschränkung (vor allem Feldmäuse)durch Greifvogel (Mäuse-, Rauhfussbussarde, Turmfalken u.a.) kann diesen, besonders in futterarmen Perioden, sehr wirksam geholfen werden. Verschiedene Arten von Greifvögeln benutzen die etwa 1 m hohen und mit einem ca. 20 cm langen Querholz versehenen Sitzkrücken als Warte, um von dort aus die Nahrungssuche zu betreiben. Die in den letzten Jahren zunehmende Entfernung natürlicher Aufbaumungsmöglichkeiten in weiten Teilen der Landschaft macht den Einsatz dieser biologischen Methode in vielerlei Hinsicht sehr lohnend. Kaatz und Bich (1979) konnten in einer Untersuchung feststellen, dass der Mäusebesatz auf Versuchsflächen von 0.5 ha, die mit je 10 Sitzkrücken versehen waren, im Vergleich zu entsprechenden Kontrollflächen ohne derartige Warten signifikant niedriger war.

## V. Zucht, Auswilderung und Wiedereinbürgerung

Wohl etwas zu Unrecht ist die Zucht in Gefangenschaft heute ganz in den Vordergrund des Interesses gerückt und hat dabei etwas die anderen Managementtechniken in den Schatten gedrängt. Bisher konnte noch keine bedrohte Vogelart auf der Erde durch Zucht gerettet werden. Am häufigsten wird dies von der Hawaiigans (Branta sandvicensis) behauptet, von der bisher über 1600 gezüchtete Exemplare ausgesetzt wurden. Es ist bisher nicht bekannt, ob sich die Population nach Beendigung der Aussetzungen allein halten kann. Lediglich bei einigen wenigen Säugetierarten konnte eine vollständige Ausrottung durch Haltung und Zucht in Zoologischen Gärten verhindert werden.

Fehlgeschlagen ist bisher der Versuch, die vielleicht seltenste Greifvogelart der Erde, den Mauritiusfalken Falco punctatus, durch Zucht zu schützen. Der Gesamtbestand an Wildvögeln hält sich seit 1975 etwa gleichbleibend bei 15 Vögeln. Im Laufe der Jahre wurden 8 Individuen zu Zuchtzwecken gefan-

gen. Ein Junges wurde gezüchtet, aber alle 9 gefangenen Tiere starben, wobei
die Weibchen Anormalitäten der Fortpflanzungsorgane aufwiesen.

Dennoch können die bisherigen Greifvogelzuchterfolge insgesamt als ermut-
igend bezeichnet werden. Noch vor 10 Jahren wären sie beispielsweise beim
Wanderfalken wohl kaum für möglich gehalten worden. Im Osten der USA konnten
so von 1975 bis 1981 mehr als 350 in Gefangenschaft gezüchtete junge Wander-
falken ausgesetzt werden. 1981 waren mindestens 7 Paare ansässig, von denen
4 eigene Junge aufzogen. In Kanada wurden von 1970-1981 368 Wanderfalken
gezüchtet, von denen 315 ausgesetzt wurden. Hier wurde der erste Beweis er-
bracht,dass diese auch erfolgreich brüten können: Ein 1975 gezüchtetes Weib-
chen, das einem wilden Paar zugesetzt worden war, legte zwei Jahre später
10 km entfernt zwei Gelege. Sechs der sieben Eier waren befruchtet, und drei
hinzugesetzte gezüchtete Junge wurden aufgezogen. In Europa brütete das erste
ausgesetzte Paar 1982 erfolgreich im Harz. Beide Partner stammen von demsel-
ben Züchter und zogen zwei Junge gross (Saar et al., 1982).

Man muss sich stets vor Augen halten,dass Zucht und Auswilderung der ge-
züchteten Vögel nur das allerletzte Mittel sein sollten, zu versuchen, das
Aussterben einer Art zu verhindern. Es bleibt immer fragwürdig, wenn dazu
bei nicht ganz so bedrohten Arten die insgesamt nur sehr begrenzten Mittel
des Naturschutzes eingesetzt werden, die vielleicht bei anderen Projekten
sinnvoller angebracht wären.

SUMMARY

## Management to Increase Raptor Populations

Not until very recently have modern methods of population management,that
is to say the purposeful, positive influencing of populations, been tested
and applied in the case of raptors. They have become necessary because of
the decline in many species which is, in some instances, world-wide; since
the beginning of the last century the European populations have, on average,
decreased to about 1% of their former level.

Prior to the application of a particular method, investigations must be
conducted to establish the extent to which the capacity of a given habitat
is utilized by a particular species and what the limiting factors are.Under
normal conditions the latter are primarily the availability of food and
nesting-places but today the main resons for the decrease are changes in the
habitat, persecution by man and contamination by toxic chemicals.

Management techniques tried out so far can be divided into four main
groups: 1. Increasing the number of nesting-places and increasing their se-
curity. 2. Increasing the reproduction rate. 3. Reducing mortality and con-
tamination by pesticides. 4. Introducing.or re-introducing to the wild rap-
tors bred in captivity. The basic prerequisite for effective application of
the individual techniques is protective measures in the classical sense, such
as legal protection and preservation of the habitats.

R e f e r e n c e s

Berggren W. - Var Fagelvarld, 1975, 34, p. 67-68.
Bijleveld M. Birds of prey in Europe. L.: MacMillan Press, 1974.

Cell M.W. Habitat Management Guides for Birds of Prey. Bureau of Land Management, U.S. Department of the Interior Technical Note, Denver, 1979.

Cavé A.J. - Netherlands J. Zool., 1968, 18, p. 313-407.

Fyfe R.W., Armbruster H.I. Raptor Research and Management in Canada. World Conf. on Birds of Prey. Ottawa, 1977, p. 282-293.

Fyfe R.W., Armbruster H., Banasch U., Beaver L.J. - In: Endangered Birds: Management Techniques for Preserving threatened Species / Ed. by S.A.Temple. University of Wisconsin Press, Madison, 1978.

Helander B. Havsörnen i Sverige. Uddavalla, 1975.

Kaatz Ch., Bich Th. - Beitr. Vogelkd., Leipzig, 1979, 25, p. 346-352.

Kennedy R.S. Transactions of the North American Osprey Research Conf., 1977, p. 35-42.

Meyburg B.-U. - Beitr. Vogelkd., 1971, 17, p. 207-227.

Meyburg B.-U. Conference on Birds of Prey, Vienna 1975. Report of Proceedings. Vienna, 1977, p. 387-391.

Meyburg B.-U. - In: Endangered Birds: Management techniques for threatened species / Ed. by S.A.Temple. Madison: University of Wisconsin Press, 1978a, p. 195-200.

Meyburg B.-U. - In: Geer Bird of Prey Management Techniques / Ed. by Oxford, Brit. Falconers' Club, 1978b, p. 81-93.

Meyburg B.-U., Garzón Heydt J. - Ardeola, 1973, 19, p.105-128.

Monneret R.J. - In: Bird of Prey Management Techniques / Ed. by T.A.Geer. Oxford, 1978, p. 56-61.

Nelson M.W., Nelson P. Power Lines and Birds of Prey. World Conf. on Birds of Prey. Ottawa, 1977, p. 228-242.

Nethersole-Thompson D. - OoL. Rec., 1931, 11, p. 73-80.

Newton I. Population Ecology of Raptors. Berkhamsted, T. and A.D.Poyser.1979.

Olendorff R.R., Motroni R.S., Call M.W. U.S. Dept. of the Interior-Bureau of Land Management Technical Note. N.Y., 1980.

Olendorff R.R., Miller A.D., Lehman R.N. - Raptor Research Report N 4, 1981.

Piechocki R. Der Turmfalke. A. Ziemsen Verlag, Wittenberg-Lutherstadt, 1970.

Saar Ch., Trommer G., Hammer W. Der Wanderfalke. Bericht über ein Artenschutzprogramm - Methoden, Ziele, Erfolge. Bonn, Deutscher Falkenorden, 1982.

Saurola P. - In: Bird of Prey Management Techniques / Ed. by T.A.Geer. Oxford: Brit. Falconers' Club, 1978, p. 72-80.

Schilling F., Böttcher M., Walter G. - J. Orn., 1981,122, p. 359-367.

Schmidt Ph. - Schweiz. Naturschutz, 1948, 14, p. 105-113.

Sothmann L. Greifvögel und Jagd. Themen der Zeit Heft 2, Kilda-Verlag, Greven, 1978.

Spitzer P.R. - In: Endangered Birds / Ed. by S.A.Temple. Madison: Univ. of Wisconsin Press, 1978, p. 171-182.

Svehlik J., Meyburg B.-U. - J. Orn., 1979, 120, p. 406-415.

Wittenberg J. Nachgelege bei Raubvögeln. Vogelwelt, 1964.

Zimmerman D.R. To save a bird in peril. Coward, McCann and Georghegan, New York, 1975.

# RECENT DEVELOPMENTS IN THE STUDY OF RAPTOR POPULATIONS

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The effective conservation of raptors requires, among other things, a thorough understanding of their population dynamics. Reproduction has been well studied, but much less is known about mortality and other aspects relevant to the construction of life tables. In these respects, studies on diurnal raptors have lagged behind those on some other birds. In this paper, I shall discuss three aspects of raptor population studies, which depend on the marking of individual birds, and on which ideas have changed recently in the light of fresh information. These include the fidelity of breeders to their nesting territories, the mortality of breeders, and the age of first breeding. I shall draw mainly on studies of Sparrowhawks _Accipiter nisus_ and other raptors by myself and colleagues in south Scotland, but will also quote some other published work where relevant.

## FIDELITY TO NESTING TERRITORIES

Many raptor species can be found nesting in the same places over long periods of years. Such places may be cliffs, isolated trees, groves of trees, or patches of forest or ground cover, depending on the species. Particular cliffs are known to have been used annually by successive pairs of eagles or falcons for periods of 70-100 years (Newton, 1976). Among 49 British Perigine _Falco peregrinus_ cliffs known to falconers between the sixteenth and nineteenth centuries, at least 42 were in use during 1930-39 (Ferguson-Lees, 1951).Continued occupancy may thus have held at many cliffs for centuries, long before there were ornithologists to record it. In trees, too, certain eagle nests have been used for longer than a man's lifetime and, added to year after year, have often reached enormous size. One historic Bald Eagle _Haliaetus leucocephalus_ nest in America spanned 8 $m^2$ on top and contained '2 waggon loads' of material, while another was 3 m across and 5 m deep (Bent, 1938). Some Osprey _Pandion haliaetus_ nests were in continued use for periods of 45, 44 and 41 years, and Red-Shouldered Hawk nests for 47 an 37 years (Bent, 1938). Certain patches of forest (though not the same nests) have been used for long periods by other species, and even patches of ground cover were used by Hen Harriers for more than 50 years (Balfour, 1957). In general, of course, sites on rock must be more permanent than those in trees, and sites in trees more permanent than those in herbaceous cover.

The continued use of particular sites by certain breeding raptors has given rise to the ideas that: (a) the same individuals are present year after year, remaining faithful both to territory and to mate, and that (b) each individual, after the death of its mate, attracts another partner to the same site, thus ensuring continuity of occupation (e.g. Tinbergen, 1946). These views gained credance from the fact that certain individual birds, which were recognised by some peculiarity of behaviour, plumage or egg type,occupied particular territories for long periods. Only in recent years, however, have these ideas been checked by use of marked individuals. The findings have revealed wide variations in fidelity to territory between populations.

Such studies entailed trapping and marking the occupants of certain terri-

Table 1. Turnover of Sparrowhawks on particular territories

| Years between captures on the same territory: | One | | Two | | Three | |
|---|---|---|---|---|---|---|
| Occupant same (S) or different (D) | S | D | S | D | S | D |
| Males. Numbers | 25 | 33 | 4 | 16 | 0 | 12 |
| Estimated annual turnover | 57% | | 55% | | - | |
| Females. Numbers | 148 | 148 | 12 | 50 | 4 | 16 |
| Estimated annual turnover | 50% | | 56% | | 42% | |

tories in restricted study areas,then cheking for the presence of these same birds in future years. They tell us about the turnover of birds at particular territories, and about shifts between territories within study areas, but they miss any birds which might have moved outside the study areas between one year and the next. Also, because female raptors spend more time near the nest than males, females are the easiest to catch and have usually provided most information.

I shall start with the Sparrowhawk, which has been found nesting in the same places for periods of 30-50 years, while ever the woods concerned remained suitable. Newton and Marquiss.(1982) studied the turnover at particular territories in south Scotland for ten years. Each time a bird was caught, note was made whether it was the same individual that was on that territory previously. From territories where occupants were identified at one year intervals, 57% of cocks and 50% of hens had changed by the second year. This gave average periods of residence on territories of 1.4 and 1.5 years respectively. The fewer records from territories where birds were caught at intervals of 2-3 years gave roughly similar estimates of turnover (Table 1).

Table 2. Periods that individual Sparrowhawks were resident on particular territories during a 10-year study

| | Number of birds present for following periods (years) | | | | | | Mean period |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | |
| Males | 42 | 8 | 1 | 1 | 0 | 0 | 1.3 |
| Females | 173 | 22 | 7 | 4 | 1 | 1 | 1.3 |

The figures just quoted gave estimates of the mean turnover of individuals from year-to-year changes, but many birds were identified in several different years. Periods that individuals were known to be resident on particular territories are given in Table 2. Only those birds which were known to start and end their stay on a particular territory within the ten year study are included. Such data are probably biassed slightly in favour of short periods, because long periods were more likely to overlap the start and end of the study, and so be excluded. This may be why the mean periods of residence, at 1.3 years for both sexes, were slightly shorter than the means calculated above from the year-to-year changes. However, the results were interesting in again showing the shortness of the periods involved. The majority of birds retained the same territories for only a year or two, and only occasional in-

T a b l e  3. Fidelity to territory among individual raptors identified in
successive years

| Species and sex | | Number of individuals in second year | | Reference |
|---|---|---|---|---|
| | | On same territory | On different territory (%) | |
| Sparrowhawk | male | 25 | 7(22) | Newton, Marquiss,1981 |
| | female | 158 | 67(30) | |
| Kestrel[*] | male | 15 | 3(17) | Village, 1980 |
| | female | 5 | 7(58) | |
| Merlin[*] | male | 9 | 3(25) | Hodson, 1975 |
| | female | '2 | 8(80) | |
| Peregrine | male | 6 | 0(0) | Mearns,Newton, 1983 |
| | female | 61 | 7(10) | |

[*] Sex difference statistically significant on Fisher's Exact Test:
  Kestrel, $P = 0.022$; Merlin. $P = 0.014$.

dividuals for up to four years (cocks) or six years (hens). Four other cocks
had been resident  for  3, 4 and 5 years when the study ended, so their pe-
riods may have been even longer. Similarly, three other hens had been resi-
dent for 6 years, and two others for at least 5 years, when the study ended.

It came as a surprise that, in this species, whose nesting places are
used over several decades, the mean individual residence periods were so
short. Evidently, the continued occupancy was produced by many different in-
dividuals occupying the same territories in quick succession, each for a
short time. Some territories were occupied in all ten years of the study,but
by a different hen each year.

Part of this high turnover was due to mortality. More than one-third of
breeding  Sparrowhawks died each year, so in a stable population, one might
expect that this proportion of places would become available for re-occupat-
ion each year. In addition, however, some birds changed territories from
year to year, thus further contributing to turnover. Overall, about 78% of
32 re-trapped males and 69% of 225 re-trapped females were in the same ter-
ritory the second year, and the remainder of each sex had moved to a diffe-
rent territory (Table 3). These figures suggested that cocks were slightly
more sedentary than hens, but in fact the difference between the sexes was
not statistically significant.

The nesting places of neighbouring pairs were sometimes as close as 0.4 km.
Many birds made only this minimum move, and beyond this, records became stead-
ily less frequent with increasing distance. In general, hens which changed
territories moved further than cocks. The median distance moved by 96 hens
was 1.5 km; most had moved less than 9 km, but one had moved 16.5 km and
another 27 km. The median distance moved by 14 cocks was 0.8 km; most had mo-
ved less than 2.0 km, but one had moved 3 km and another 19 km. Possibly the
longer movements of each sex were underestimated, if they took birds out of

T a b l e   4. Proportion of hens which changed territory, according to age and nest success the previous year. Birds which failed the previous year more often changed territory than did birds which succeeded, but the tendency to change territory became less marked with increasing age

| | Comparison between following ages (years) | | | | | |
| | 1-2 | | 2-3 | | 3+ to following year | |
| | On same territory | On different territory | On same territory | On different territory | On same territory | On different territory |
|---|---|---|---|---|---|---|
| After success in previous year | 6 | 5 | 16 | 5 | 103 | 26 |
| After failure in previous year | 0 | 10 | 4 | 5 | 19 | 16 |
| Significance of variation within age groups | $x^2 = 5.2$, $P < 0.05$ | | $x^2 = 1.6$, $P < 0.3$ | | $x^2 = 0.8$, $P < 0.5$ | |

the study area; in general, however, movements were short compared to those which could have been recorded in the study areas concerned (two areas measuring 40 x 20 km and 20 x 12 km, and 15 km apart at their nearest points).

What circumstances led birds to change territory? Both sexes more often changed territories if they had failed in their breeding the previous year than if they had succeeded  but this result was statistically significant only in hens. Thus, of 161 retrapped hens which had produced young the previous year, 22% changed territory, while of 54 which failed, 57% had changed territory. The tendency to move after a failure was especially marked between the first and second year of life in hens, and became less marked with age (Table 4). Older hens showed a strong tendency to stay on the same territories, whether successful or not the year before. Among cocks, the number of one-year-olds was very small, but among older birds the same trend held as in hens, with greater residence with increasing age (Table 4). In both sexes, movements became shorter with increasing age. So not only were old birds less incluned to change territory than young ones, when they did change, they moved less far.

One further factor which influenced movements was territory quality (a high grade territory was one where nest success during the ten year study was good). Both yearling and adult hens showed a strong tendency to stay on high grade territories after a success, and to move away from low grade territories, irrespective of whether the previous attempt was successful or not.

The frequent deaths and movements meant that most Sparrowhawks had a different mate each year. Birds which changed territory almost invaribly changed mates as well, even though in many cases the original mate was still alive,on the original or a different territory. However, some partners remained together on the same territory, and four years was the longest period·recorded.

Summarising, most Sparrowhawks which survived from the previous year stayed on the same territory, but some moved,particularly hens which failed the previous year, which were yearlings the previous year, or which were on poor ter-

ritories the previous year. The site fidelity was related to the age and pre-
vious success of the bird, and to the quality of territory. A change of ter-
ritory was almost invariably associated with a change of mate.

In two small falcons that have been studied in detail, some individuals
also changed territories between years, again females more often than males.
Among Kestrels Falco tinnunculus in south Scotland, 18 males were identified
in successive years, 15 on the same territories and 3 on different territories,
whereas of 12 females, 5 were on the same territories and 7 on different ones
(Village, 1980). The sex difference in frequency of movement was statistically
significant (P = 0.022, Fisher's Exact Test), but not the distances moved. In
both sexes, these distances averaged less than 2 km in a study area where move-
ments up to 15 km could have been recorded. Kestrels were partial migrants in
this area, and males much more often stayed on their territories over winter
than did females, most of which left. In the Netherlands, Kestrels varied in
behaviour, according to changes in the numbers of the rodents which formed the
main food (Cavé, 1968). When Kestrels were on the increase, up to 70% of
adults returned to the study area from one year to the next, but when they
were on the decline, as few as 10% of birds returned.

Among Merlins Falco columbarius in Alberta, 12 adult males were re-trapped,
9 on the territory where they had previously bred, 2 on territories less than
4 km away and the other 12 km away. But of 10 adult females, only 2 were on
the same territory, 3 were on territories less than 15 km away, 3 were 15-
30 km away, while 2 were more than 100 km away  (Hodson, 1975). Again, the
sex difference in frequency of moves was statistically significant (P = 0.014,
Fisher's Exact Test).

For these three species, neither of the ideas on territory and mate fideli-
ty mentioned at the start of this section held in an unqualified manner. Al-
though the same places were used for nesting in different years, this could
not always be attributed to the return of the same individuals, and birds
often changed their nesting territories, irrespective of what their former
mates did. Moreover, some territories were occupied by completely different
pairs from one year to the next, and others were vacant for one or more years,
before being re-used. Almost certainly, the same places continued to be used
for nesting because they were particularly good places within the local lands-
cape and territorial framework, rather than through continuity of individuals.

Other raptors have shown much greater fidelity to territory. Among Peregri-
nes in south Scotland, 6 males were trapped in successive years, all on the
same territories, and 68 females were trapped in successive years, 61 on the
same territories. Four of the seven which moved were found on adjacent terri-
tories, 3-10 km away, but the others had moved further afield, up to 33 km
away in an area where movements exceeding 170 km could have been recorded. Si-
milarly, among Ospreys in eastern North America, individuals typically retur-
ned to the same nest site, or one within 2 km, for many years in succession.
Only 3% of returning adults moved further than this, up to 18 km (Spitzer,
this symposium).

The most extreme fidelity to territory and mate was shown by some Greater
Kestrels Falco rupicoloides studied in the Transvaal (A.C.Kemp, in Newton,
1979), in which ten pairs remained on their territories over a 3-year study

698
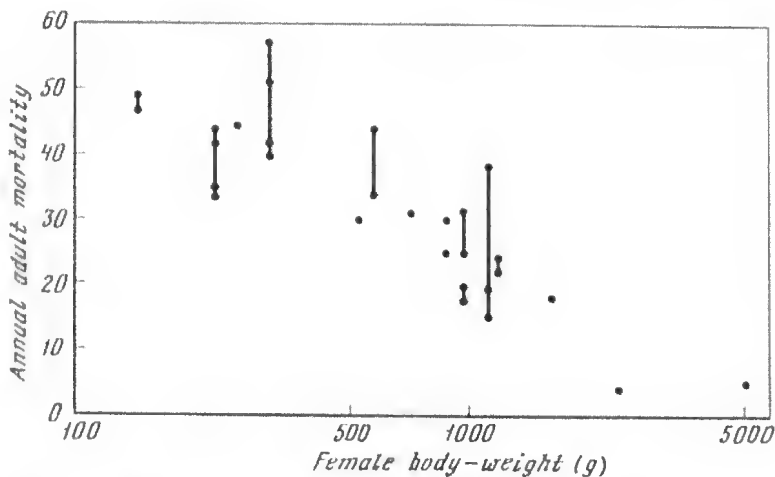
F i g. 1. Annual mortality of adult raptors shown in relation to female body weight. Mostly based on ring recoveries, lines join different estimates for the same species

period, with only one replacement of a male which died. Thus these birds showed not only great fidelity to territory and mate, but also exceptionally high survival. Similar data on smaller samples had been published for Hobbies Falco subbuteo and various Buteo species, including B.platychtarus and B.galapagoensis (Matray, 1974, de Vries, 1975).

MORTALITY

Most existing estimates of annual mortality in raptors are based on the ring recoveries of birds found dead, and reported by members of the public. Such estimates have revealed the general trend in Figure 1, for mortality to correlate with body size, the smaller species showing greater annual mortality in adult life than the larger ones. This fits the trend in other birds, and would be expected from reproductive rates. However, some of the estimates obtained in this way for raptors have long been in doubt, because in some species the estimates are so large that, on known reproductive rates, the populations concerned would soon have become extinct, yet in reality they continued to thrive. This is particularly true for species which are often shot, such as some accipiters and harriers.

The recent trapping of adults on nesting territories in successive years has provided other estimates of mortality among breeders, but again the data are more numerous for females than for males. In female Sparrowhawks, estimates were obtained (a) from the ratio of different age classes in the breeding population, in which most nestlings had been ringed during twelve years of study, and (b) from the recovery frequency of particular females in successive years (Newton et al., 1983). On the ratio method, the mortality of adult females was estimated at 36% per year, and on the recapture method, it was estimated at 34%. A similar figure obtained by recapturing individual Peregrines in successive years gave a mortality estimate of 11% per year (Mearns, Newton, 1983).

These estimates are all maxima, because they do not allow for any birds

699

T a b l e  5. Annual mortality of adult raptor (2+ years) calculated (a)
from local etudies on marked breeders eeen alive and (b) from widespread
ringing programmee relying on reporte of birds found dead

| | Local studies of breeding adulte | | | Wideepread ringing programmee | | |
|---|---|---|---|---|---|---|
| | Annual adult morta- lity | Locality | Source | Annual adult morta- lity | Locality | Source |
| Osprey | 10-15% | E.United States | Spitzer, 1980 | 18% | E.United States | Henny, Wight, 1969 |
| Sparrowhawk | 35% | S.Scotland | Newton,Mar- quise,Ro- thery,1983 | 42% | Germany | Kramer,1973[*] |
| | | | | 51% | W.Europe | Tinbergen,1946 |
| | | | | 40% | Denmark | Shelde,1960 |
| | | | | 57% | Britain | Newton,1975 |
| Peregrine | 11% | S.Scotland | Mearne, Newton, 1983 | 32% | Sweden | Lindberg, 1977 |
| | | | | 25% | United Statee | Enderson,1969 |
| | | | | 29% | Finland | Meba, 1971 |
| | | | | 28% | Germany | Meba, 1971 |

[*] Calculated by me from data in Kramer (1973).

which may have moved outeide the etudy areae to breed eleewhere. Nonetheless,
they are coneiderably lower than those made from general ring recoveries
(Table 5). The two typee of recoveriee are from largely different eectore of
the population. The general ring recoveries are moetly from birds found dead,
often killed by man, and often weighted heavily towarde the younger age clas-
ees. The eetimatee from particular etudiee refer to breeding adulte in res-
tricted areas, over ehorter time periode. They thue repreeent the "better
quality" individuale within a population. The estimate for the Sparrowhawk
wae from a elightly declining population, while that for the Peregrine was
from an increaeing population. The varioue eetimates from national ring re-
coveries were from populations that were fairly etable during the period
from which all, or almoet all, ring recoveriee came. Relatively few recove-
riee were included from the organochlorine peeticide era, when populatione
declined. Perhape the main leseon ie that eatimates obtained in either of
theee waye cannot readily be extrapolated to the whole population, whatever
ite trend. Similar differencee have been found in eome other birds, in which
mortality hae been eetimated in both waye (e.g. Perrine, 1971).

In the absence of marked birds, the mean mortality in certain populations
hae been calculated from a knowledge of adult numbere over several years,and
of the production of young. The method depends on the fact that, in any
stable population, the birthrate must equal the deathrate. It telle ue noth-
ing of how mortality ie distributed between different age claeeee, and beco-
mee complicated when account must be taken of movemente. It hae been ueed on
the ieolated population of Red Kitee Milvus milvue in Wales, in which the
mean annual mortality was eetimated at 17% (Davies, Davis, 1973), and more
recently on a population of Oepreys in eastern North America, in which the
mean annual mortality of adult (2+) birde wae estimated at 10-15% (Spitzer,

this symposium). Populations of both species were increasing during the years concerned, and again the estimate for the Osprey was lower than one produced from general ring recoveries (Table 5). To my knowledge, no estimate from ring recoveries has been published for the Red Kite.

AGE OF FIRST BREEDING

A third aspect on which recent ringing has changed traditional ideas is the age of first breeding, and its relationship to plumage changes. Most small and medium-sized raptors achieve definitive "adult" plumage in their second year of life, though some medium sized species probably not until their third year. Only the large eagles, vultures and condors take until their 4th-9th years, depending on species (Newton, 1979). Almost all our information on plumage changes in large raptors has come from captive individuals only, but in some smaller species, findings on captives have been amply confirmed on wild birds.

Most raptors seen at nests are in "adult" plumage, so this has provided minimal estimates of the age of first breeding, when the age at which adult plumage is acquired is known in the species concerned. However, many small and medium sized species have nested in "juvenile" or "immature" plumage, showing that at least some individuals breed before the age at which they don the adult dress. This is frequent among small accipiters, falcons and others, and occurs occasionally among medium and larger raptors, including eagles (Newton, 1979). In those species studied in detail, breeding in "immature" plumage was more frequent in females than in males, more frequent in good than in poor food conditions, and more frequent in depleted than in saturated populations (Newton, 1949).

Recent studies of ringed birds have provided more precise information,and shown that age of first breeding is highly variable within populations. In each study, a bird was considered a first-time breeder, providing that (a) it was new to a particular territory, (b) it (or its mate) laid one or more eggs, (c) it was not previously known to have bred elsewhere. Because occasional individuals may have changed territories from outside the study areas, these figures gave maximum estimates of age of first breeding, but territory changes were so infrequent in most species (see above), that the figures should not be greatly in error. In some of the larger species, certain individuals had occupied a territory in the previous year, without producing eggs.

Among female Sparrowhawks found breeding for the first time, 49 (26%) were in their first year of life, 62 (33%) in their second year, and 78 (41%) at a later age. Among male Peregrines, 4 birds first bred at 2 years old, one at 3 years, and another at 4 or 5; among females, 2 birds first bred at one year old, 13 at 2 years and one at 3. Another 5 yearling females were seen in the breeding population without being caught, but no yearling males. These data suggest that males may start, on average, at a later age than females (as found in captive Peregrines, Cade, Fyfe, 1977), but the sex difference was not statistically significant. In Red Kites, 5 birds first bred at 2 years old, one at either 2 or 3, 3 at 3 years old, one at 4 or 5 (Davis,Newton, 1980). In Ospreys, 10 individuals bred in their third year, 3 in their

fourth and 2 in their fifth (Spitzer, this symposium). These four species
acquire adult plumage in their second year.

These various records show that age of first breeding is highly variable
within species, and confirm that many birds may spend one or more years in
full adult plumage before attempting to nest. In this respect, these raptors
resemble some large seabirds. Factors which may lead to delayed breeding in-
clude: (a) inability to acquire a suitable territory or mate, in an area in
which all suitable territories and mates are taken, or (b) inability to accu-
mulate the body reserves necessary to breed, itself partly a result of the
food situation (Newton, 1979). Either way, the ability of a given raptor in-
dividual to breed is not necessarily linked with gonad maturation. In small
species, the gonads may be functional in the first year of life, yet breed-
ing delayed for one or more years for the reasons just given. Some first-
year male Sparrowhawks, which were not breeding, had testes as well develo-
ped as other first-year and adult males which were breeding (unpublished da-
ta). Thus, the age at which the gonads can produce active sperm or ova, the
age at which adult plumage is acquired, and the age of first breeding are
best regarded as largely independent events in raptors, only poorly correla-
ted in any one population. The only invariable condition is that first gonad
development should coincide with, or precede, first breeding. General terms
such as "age of maturity" are therefore best avoided, and replaced by more
specific terms, relating to the gonads, plumage or breeding, as the case
may be.

There may also be problems in judging age from plumage changes. In large
raptors, such as Aquila eagles, each generation of feathers may take more
than one year to replace, and individuals may be in active moult for most of
their pre-breeding lives. In such species, the age at which definitive adult
plumage is acquired may itself be variable, depending on how quickly the bird
has passed through previous plumages. Existing knowledge of plumage changes
is based on small numbers of well-fed captive birds, as mentioned, but in-
spection of wild and museum birds reveals very different rates of moult (num-
bers of feathers in growth) in different individuals, and at different times.
Thus some individuals may pass through a fixed number of plumages more
quickly than others, and acquire their adult plumage at an earlier age. To
my knowledge, no-one has demonstrated this in the field, but it is a clear
possibility, which signals the need for caution in judging ages from pluma-
ges in large species.

CONCLUSIONS

Despire the continued use of particular nesting places, which is such a
striking feature of many raptor populations, the extent to which this invol-
ves the return of the same individuals from year to year varies greatly bet-
ween populations. Changes of territory were common among the individuals of
some of the species studied, yet rare in others. In one species, movements
were found only in females, and in others they were more frequent in females
than in males. In Sparrowhawks and Kestrels, they also varied according to
territory quality and food supply, birds staying more frequently in good than
in poor conditions, and with age, with old birds staying more often than

young ones. On the other hand, fidelity to territory was not related to whether a species was resident or migrant, as extremes of behaviour were found in both groups. Greater fidelity would of course be expected in populations that were stable in numbers and distribution from year to year than in populations which were continually changing in relation to fluctuating food-supplies.

None of the other phenomena discussed in this paper were unexpected, as they could have been predicted from studies on other birds. However, the mortality estimates from breeders, which are given here, are the first available for any diurnal raptor, as are the estimates of age of first breeding in birds in adult plumage. A major need now is for similar studies on large eagle species, as these birds are likely to be extreme by any standard in their low mortality and long pre-breeding periods. In recent years, with so many populations depleted by pesticide poisoning, attempts have often been made to model populations, using precise statistics on breeding, but only rough approximations on other population parameters. Studies of the type described here should emphasise the weakness of existing models, as well as help to improve future ones.

SUMMARY

1. This paper reviews findings on fidelity to territory, adult survival and age of first breeding in raptors, based on recent studies involving marked adults.

2. The turnover of Sparrowhawks on territories was high, with 57% of males and 50% of females changing between one year and the next. Mean residence periods were 1.4 and 1.5 years respectively, but some males stayed on the same territories for up to 5 years and some females for up to 6. Turnover was due mainly to mortality, but partly to movement. Changes of territory were most frequent among young birds, among birds which were on poor territories, and among birds which failed in their breeding the previous year.

3. Among other raptors, species varied in the degree to which individuals stayed on the same territories from year to year. Changes of territories were frequent among Kestrels and Merlins, but rare among Peregrines and Ospreys. However, in all species in which the point was examined, males more often stayed on the same territories than did females.

4. Mortality based on recaptures of breeders in successive years was estimated at about 35% for Sparrowhawk females, and 11% for Peregrines (both sexes), while using a different method it was estimated that 15% for Ospreys (both sexes) and at 17% for Red Kites (both sexes). These estimates are lower than those obtained for adults of the same species in widespread ringing schemes, in which most recoveries are of birds found dead by members of the public.

5. Age of first breeding was highly variable within populations. Among Sparrowhawk females found breeding for the first time, 49 were in their first year of life, 62 in their second year and 78 in a later year. Among Peregrines (both sexes), 2 were in their first year, 17 in their second year, 2 in their third year, and one in its fourth or fifth year. Among Ospreys (both sexes) 10 were in their first third year, 3 in their fourth and 2 in their

fifth year; while in Red Kites (both sexes), 5 were in their second year, one
was in its second or third year, 3 were in their third year, and one in its
fourth or fifth year.

R e f e r e n c e s

Balfour E. - Bird Notes, 1957, 27, p. 177-183, 216-224.
Bent A.C. Life histories of North American birds of prey. Vol. 1, 2. New
    York: Dover, 1938.
Cavé A.J. - Netherlands J. Zool., 1968, 18, p. 313-407.
Davies P.W., Davis P.E. - Br. Birds, 1973, 66, p. 183-224, 241-270.
Enderson J.H. - In: Peregrine Falcon populations: their biology and decline /
    Ed. by J.J.Hickey. Madison, Milwaukee and London: Univ. Wisconsin Press,
    1969, p. 505-508.
Ferguson-Lees J.L. - Bird Notes, 1951, 24, p. 200-205, 309-314.
Henny C.J., Wight H.M. - Auk, 1969, 86, p. 188-198.
Hodson K.A. The ecology of Richardson's Merlins on the Canadian Prairies.
    M.Sc. thesis. University of British Columbia (Vancouver), 1975.
Kramer K. Habicht und Sperber. Die neue Brehm-Bücherei. Wittenberg Luther-
    stadt: Ziemsen Verlag, 1973.
Lindberg P. The Peregrine Falcon in Sweden. Proceedings ICBP World Conference
    on birds of prey, Vienna, 1975. Vienna, 1977, p. 329-338.
Matray P.F. - Auk, 1974, 91, p. 307-324.
Mearns R., Newton I. Turnover and dispersal in a Peregrine population, 1983.
Mebs Th. - Die Vogelwarte, 1971, 26, p. 98-105. German, with English summary.
Newton I. - Brid Study, 1975, 22, p. 35-43.
Newton I. - Canad. Field-Nat., 1976, 90, p. 274-300.
Newton I. Population ecology of raptors. Berkhamsted: Poyser, 1979.
Newton I., Marquiss M. - J. Anim. Ecol., 1982, 51, p. 327-41.
Newton I., Marquiss M., Rothery P. Age structure and survival in a Sparrow-
    hawk population, 1983.
Perrins C.M. - Bird Study, 1971, 18, p. 61-70.
Schelde O. - Dansk. Orn. Foren. Tidsskr., 1960, 54, p. 88-102.
Tinbergen L. - Ardea, 1946, 34, p. 1-123.
Village A. The ecology of the Kestrel (Falco tinnunculus) in relation to
    vole abundance at Eskdalemuir, south Scotland. Ph.D. thesis, Edinburgh
    University, 1980.
Vries De Tj. - Le Gerfaut, 1975, 65, p. 29-57.

INITIAL POPULATION RECOVERY OF BREEDING OSPREYS (<u>PANDION HALIAETUS</u>)
IN THE REGION BETWEEN NEW YORK CITY AND BOSTON

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## HISTORICAL BACKGROUND

During this century and the last, the coastal zone between New York City
and Boston, Ma.supported some of the highest recorded densities of nesting
ospreys in the world.    At least 1.000 nests are estimated to have been
active in the early 1940's (Spitzer, Poole, 1980). Typical reproductive rates
in the 1930's and early 1940's ranged from 1.0–2.0 young fledged per active
nest (defined as a nest in which eggs are laid) (Wilcox, 1944; Peterson,1969;
Puleston, 1977; Spitzer et al., 1978).

During the 1950's and 1960's, this population suffered extremely poor
reproduction, associated with DDE residues in eggs and abnormally thin egg-
shells (Wiemeyer et al., 1975; Spitzer et al., 1977). The first precise ob-
servations, made in the period 1957–1962 in portions of Connecticut and
eastern Long Island, N.Y., averaged 0.2–0.4 young fledged per active nest
(Ames, Mersereau, 1964). This is though to be typical of most of the popu-
lation at that time. With reproductive rate a small fraction of what was con-
sidered normal, natality was inadequate to balance mortality. The population
"crashed", declining at perhaps 10% each year. Concentrations of nest in the
Connecticut River estuary, Ct., and Narragansett Bay, R.I., were declining
at rates of up to 30% per year (Ames, 1966), implying local adult death rates
far higher than normal. By 1969, the number of active nests in the region was
reduced to about 150, roughly 15% of the 1,000 estimated 25 years previously.
(See map of study region - Figure 1.)

## THE STUDY PERIOD 1969-1981

During the period 1969–1981,Spitzer, Poole, Scheibel, many cooperators,and
state agencies recorded active nests and young fledged in the region. The
region's accessibility, the virtually complete restriction of breeding osp-
reys to the coastal zone, and the abundance of good observers allowed near-
total counts of these two population parameters (Spitzer, 1980). Trends in
these parameters can be summarized as follows (see also Figure 2):

1. Reproduction in 1969 was 0.53 young fledged per active nest, and had
probably already increased to about twice the rate of the early and mid-
1960's (Spitzer, 1980).

2. Reproduction increased steadily to 1.55 young per active nest in 1981.
The first part of this increase is known to have coincided with sharply dec-
lining DDE concentrations in eggs (Spitzer et al., 1978). Unfortunately, no
eggs have been analyzed for DDE since 1976.
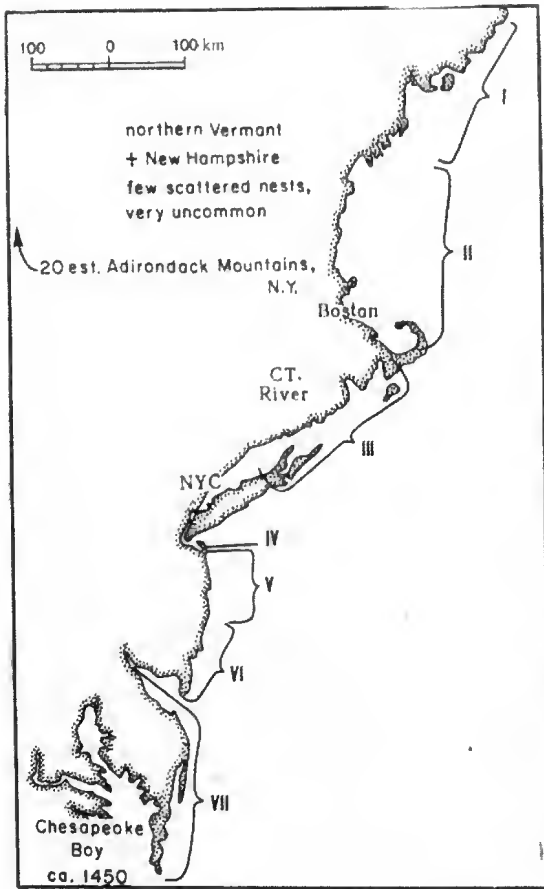
Fig. 1. Map showing geographical isolation of the study population

I - 200 plus est Maine coast, beginning at Casco Bay, just NE of Portland; II - 0? southern Maine coast to northern Cape Cod - no active nests known; III - 109 the population under study; IV - Sandy Hook + Navesink River, N.J.; V - 6 Manasquan R. to Barnsgat Light, N.J.; VI - 53 southern N.J. coast (mostly Cape May County); VII - 153 Atlantic coast of Delaware, Maryland, + peninsular Virginia

1975 data are used because precise surveys of brseders were carried out betwsen N.Y. City and Chesapeake Bay in that year (see Henny st al., 1977)
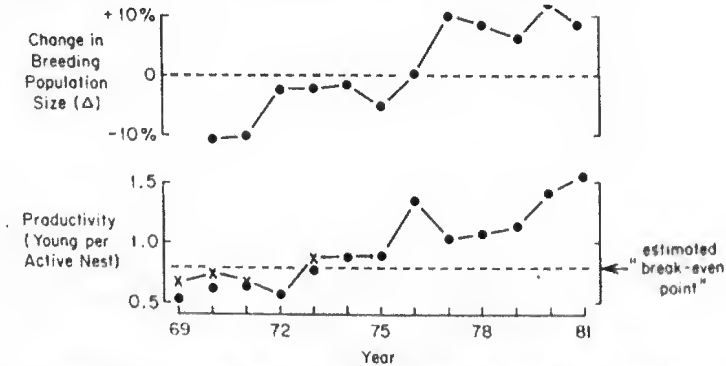


Fig. 2. A comparison of Osprey reproductive rate and change in population size, N.Y. City to Boston, 1969-1981. Points dsnoted by "X" on ths lower graph are productivity values which include young introduced from Maryland by Spitzer (1978)

3. The active nest count showed an annual decline of about 10% in both 1970 and 1971 (Spitzer, 1980). This was a continuation of the "crash" of the late 1950's and the 1960's, with natality inadequate to balance mortality of breeders.

4. From 1972 through 1975, the annual decline in active nests averaged 3%. Allowing for the 3 to 5 years between fledging and first-breeding (Spitzer, 1980), we hypothesize that local natality was at levels nearly adequate to balance mortality. There was no evidence of excessive, toxin-related adult mortality in this period. In the years 1968-1973, local natality was boosted by introductions of eggs and nestlings from the Chesapeake Bay region (Figure 2) (Wiemeyer et al., 1975; Spitzer, 1978).

5. In 1976, the breeding population stood at 109 active nests its low point for the 20th century. During the next five years, the breeding population showed steady annual increases ranging from 6.9 to 11.5%. The 1981 count found 168 active nests in the region.

ESTIMATION OF A REPRODUCTIVE "BREEK-EVEN" POINT

The dramatic increases observed in reproduction (young fledged) and subsequently in breeding population size (active nests) encouraged Spitzer to examine the relationship between these parameters. This required data on (1) dispersal of young between fledging and breeding, (2) regional fidelity of established breeders, and (3) age at first breeding, all of which had been collected during the study period. The effects of these variables can be summarized as follows (for details see Spitzer, 1980):

1. Dispersal distance was low, especially that of males (Table 1). Since it appears that males select the nest location (Spitzer, unpubl. data), this has the effect of tieing regional reproduction even more closely to subsequent change in population size. Nestling ospreys have been intensively banded in an arc of coastline stretching from Virginia to Massachusetts, thus permitting the potential discovery of long-distance immigrants from nesting areas south of New York City. There was no evidence of significant immigration of males from this direction, and only 2 females were recorded making such a movement. More impressive evidence of low dispersal rates came from Cape May County, New Jersey, where of 24 banded breeders trapped in 1979, only 4, all females, had fledged at nests 71-261 km away in Delaware, Maryland. and Virginia, despite 5,309 bandings in those states in the years 1955-

T a b l e 1. Relationship of dispersal to sex (From Spitzer, 1980)

| Sex | Distance between Fledging Site and Breeding Site (km) | | | |
| --- | --- | --- | --- | --- |
| | 0-10 | 10-50 | 50-200 | 200 plus |
| Females (N = 39) | 14 | 16 | 5 | 4 |
| Percentage in each category | 35.9% | 41.0% | 12.8% | 10.3% |
| Males (N = 33) | 24 | 9 | 0 | 0 |
| Percentage in each category | 72.7% | 27.3% | 0 | 0 |

Notes: a) Maximum female movement in sample is 520 km.

b) Maximum male movement in sample is 37 km.

c) Maximum distance between large-scale banding and trapping activities, thus maximum detectable movement, is 700 km.

1976 (Robichaud, in prep.). 522 bandings in Cape May County during the same
time period yielded 18 of the 24 banded breeders trapped there in 1979.

We realize that long-distance dispersal of both sexes occurs. Ospreys re-
colonized Scotland, presumably from Scandinavia (Österlöf, 1977). A color-
banded male bred at Montezuma National Wildlife Refuge in central New York
state in 1980 and 1981, the only known active nest in this region, and 425 km
from the nearest color-banding activity. However, currently available evi-
dence suggests that long distance dispersal of ospreys is occurring at low
frequency in the northeastern United States, sufficient to establish some
new breeding areas but not to have large effects on subsequent population
dynamics. The low fledging-to-breeding dispersal distance of a bird that per-
forms dramatic seasonal migration is quite remarkable. The reduced density
of some populations owing to DDT effect may reduce pressure for such disper-
sal, if indeed it is density-dependent.

Ospreys breeding to the north of our study area in Maine and Canada area
not banded intensively, and the possibility of net immigration from that re-
gion cannot be assessed from band recoveries. Many individuals from that re-
gion would pass through the study area twice a year, and ospreys linger
around at least one food-rich portion of the study area – the Connecticut Ri-
ver estuary – during fall migration. We assume that net immigration from the
north (as well as from the south) is negligible. This assumption will become
important in subsequent calculations of the population's reproductive "break-
even" point and in discussion of annual survivorship.

2. Potential movement of established breeders was studied by color-banding
a sample of breeding birds. These individuals typically returned to the same
nest site or one within 2 km for many years in succession. 3% of the retur-
ning birds moved from 2 to 18 km (N=136). No greater movements were recorded.

3. Age at first breeding was estimated by Spitzer (1980). During the course
of nest surveys, checks for breeding birds color-banded as nestlings were made
whenever possible. When such a bird was found breeding at a site where either
it had not been present the previous year, or had been a non-breeder,and when
there was no evidence that it had bred previously elsewhere in the region, it
was considered a first-time breeder. From 20 such records, the proportions of
first-time breeders were estimated at 50% three-year-olds, 30% four-year-
olds, and 20% five-year-olds.

Spitzer then calculated the young per active nest figure ("productivity")
that should most accurately reflect the level of recruitment of new breeders
in a given year (known as year "t"). He weighted the number of young fledged
3, 4, and 5 years ago (known as $Y_{t-3}$, $Y_{t-4}$, and $Y_{t-5}$) by their estimated
contribution to first-time breeders, thus: $0.5\ Y_{t-3}+0.3\ Y_{t-4}+0.2\ Y_{t-5}$. To
adjust for change in breeding population size since these young fledged, he
divided their weighted sum by the number of nests active in the year immediat-
ely before their recruitment, $A_{t-1}$. This measure of productivity ($0.5\ Y_{t-3}+$
$+0.3\ Y_{t-4}+0.2\ Y_{t-5}$) / $A_{t-1}$ he called adjusted recruitment productivity, or
"A.R.P.$_t$".

Calculating A.R.P. for the years 1974-1981, we compare it to annual per
cent change in breeding population size, defined as $/(A_t-A_{t-1})/A_{t-1}/$ x 100 =
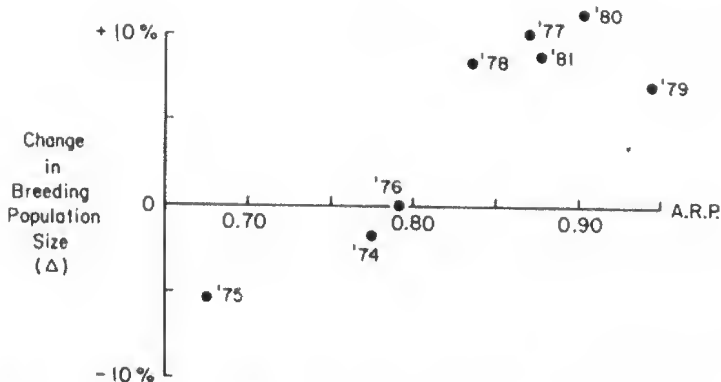
F i g. 3. Relationship between "Adjusted Recruitment Productivity" (ARP) and annual change in breeding population size, 1974-1981. From Spitzer(1980)

$= \triangle\%$. This comparison is shown in Figure 3. Without any effort to apply further mathematics or statistics to these eight data points, we argue that they suggest a production requirement for population stability of roughly 0.8 young fledged per active nest under the particular conditions of population density and age structure during the study period.

ADDITIONAL CHARACTERISTICS OF THE RECOVERING POPULATION

1. Implied High Survivorship. Using 0.8 young/active nest as the population's reproductive "break-even" point, Spitzer (1980) estimated annual survivorship rates of 59% during the first year of life ($s_0$) and a constant 85% thereafter (s). The simple equation used to make these estimates, developed by Henny and Wight (1969), does not allow for age-specific variation in survivorship after the first year of life, although such variation is common within and between populations of long-lived vertebrates (Miller, 1976; Caughley, 1977). However, the simple equation that uses only $s_0$ and s is adequate to make the point that current survivorship appears to be higher, and production requirements for population stability lower, than the estimates made by Henny and Wight (1969) based on composite dynamic life tables constructed from recoveries of ospreys banded as nestlings in the northeastern coastal region in the years 1926-47 (and recovered over the next 20 years). Such recoveries are now seldom used to estimate annual survivorship and production requirements (for details see Spitzer, 1980; Burnham and Anderson, 1979; Anderson et al., 1981).

Although a reproductive "break-even" point of 0.8 supports estimates of $s_0 = .59$ and $s = .85$, the speed with which the breeding population has increased during the last 5 years means that: (1) survivorship of some age groups has been higher than one or both of these estimates, or (b) there has been net immigration to the breeding population, or (c) some combination of these two factors has occurred. The DDT era appears to have resulted in population density being reduced faster than habitat quality - thus very high survivorship in the expanding population is perhaps not surprising. A 90% annual survivor-

ship of breeding birds (which implies that all two-year-olds and some three and four-year-olds are still surviving at 85%/year) is one pattern which would roughly account for the observed rate of population recovery. This survivorship pattern and others will be tested against the accumulating population data.

2. High Proportion of Non-laying Pairs. We define "non-laying pairs" as those which build a nest but do not lay eggs. We have observed a dramatic increase in non-laying pairs as the study population shifted from decline to growth: None were recorded in 1970, 3 in 1972, 2 in 1973, 5 in 1974, 2 in 1975, 9 in 1976, 10 in 1977, 17 in 1978, 22 in 1979, 20 in 1980, and 26 in 1981. We suggest that this trend is due to the inclusion of more young birds in the population. As proportionately more young birds return, there are proportionately fewer experienced birds in need of a new mate. Inexperienced birds may be forced to pair with each other, and although they frequently build a nest, laying of eggs may be less likely to occur. This phenomenon can be modeled with our annual data of active nest (A) and young fledged (Y). $s_0=.59$ and $s=.85$ are used, but other survivorship schedules would yield a similar pattern. In any given year "t", we are interested in the ratio of "surviving young 3 to 5 years old", the source of new breeders, to "available experienced birds", defined as those established breeders whose mates have died since the last breeding season (year t-1).

$$\frac{\text{surviving young 3 to 5 years old}}{\text{available experienced birds}} = \frac{s_0 s^2 Y_{t-3} + s_0 s^3 Y_{t-4} + s_0 s^4 Y_{t-5}}{A_{t-1} \left[1 - s^2 - (1 - s)^2\right]}$$

last year's laying pairs    neither of the pair dies    both of the pair die

$$= A_{t-1}\left[1-(0.85^2) - (0.15^2)\right] = 0.255 \ A_{t-1}$$
ont of the pair dies

$$\approx \frac{A_{t-1}}{4}$$

This ratio provides a useful measure of age structure, and we will call it the age structure ratio, or "A.S.R.$_t$". Calculating A.S.R. for the years 1974-1981, we compare it to the ratio of non-laying pairs to active nests (Figure 4). When A.S.R. is near 3.0, there are few non-laying pairs. This makes sense because only about one-third of the "surviving young 3 to 5 years old" would initiate breeding in a single year. Thus a potential one-to-one match of these with "available experienced birds" is implied by a ratio of 3.0. (It should be noted that available experienced birds may preferentially pair with one another, especially if they are in close proximity). As the ratio rises above three, the potential new breeders would begin to outnumber available experienced birds and be forced to pair with one another. During the years 1979-81, as A.S.R. approached 4.0, the ratio of non-laying pairs to active
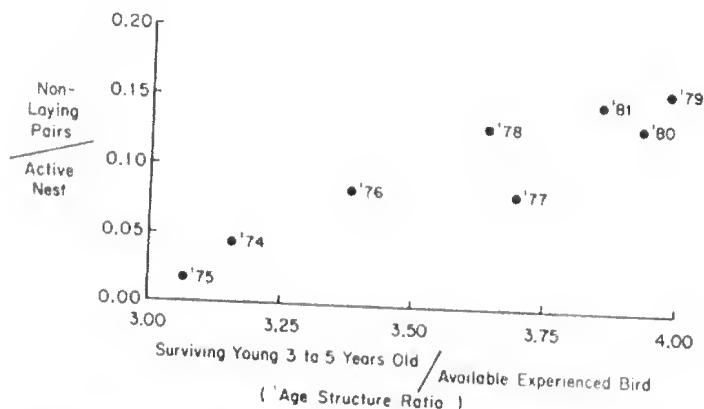
F i g. 4. Rslationehip between population age-etructure and proportion of non-laying pairs, 1974-1981. Surviving young 3 to 5 yeare old/available experiencsd bird is termed ths age structure ratio. Ses text for details, and for dsrivation of figures

nests hovered around 0.15 (Figure 4). Becauee productivity hae continued to increase, the A.S.R. should riee well above 4.0 for awhile, parhape as high ae 4.5. If non-laying paire reepond to this rise, they will riee to 0.20 or even a larger proportion rslative to the number of active neste, despite a continued riee in active neete.

3. Heavy Uee of Man-made Nesting Platforme. Moet of the increase of active neste hae occurrsd on such eites. Availability of nesting platforms has so far generally been in excees of population increase. Newton (1976, 1979) hae emphasized that neet eites and food availability are the two major factore limiting raptor populations. It appeare that natural nest sitee might now be limiting the breeding population and/or ite reproductive euccess in some localitiea. Man-made neeting platforms are providing etable, isolated (from human activity), and predator-proof nest eitee. Thie last characterietic ie eepecially important, ae raccoons (Procyon lotor) are common in much of the study areas and are known predatore of the eggs and young of Ospreys (Ames, Mersereau, 1964; Reese, 1977; Poole, 1981). Tree nests are often vulanerable to raccoone, unless the trunk ie eheathed with one metre of ruetproof metal sheeting. Thie was dramatically demonetrated in 1981 on Maehomack Point, Shelter Ie., N.Y., where 9 tree neete without predator guarde were eituated on a 35 ha peninsula. All of theee neste failed, deepite a success rate of over 70% in eurrounding areae. Raccoon predation wae the presumed cause; raccqon hair wae found on some of the failed neet trees (Scheibel pers. obs.). Raccoone are very opportunistic feedere and no doubt are maintained to a considerable degrss by foods reeulting from the dense human population in portions of the study area. Twsrs ie good reason to believe they are now much more abundant here than during the pre-DDT era. Thus raccoon predation may be expected to have a profound effect on osprey neet eite eelection, both currently and as the population continuee to expand.

CONCLUSIONS AND PREDICTIONS

High reproductive rate, rapid breeding population growth, low fledging-to-breeding dispersal, high site fidelity of established breeding birds, and implied high annual survival all indicate a population which is at low density relative to available resources. We predict a sustained recovery. In nesting areas with mammalian predators and constant human presence, much of the future increase will probably depend on predator-proof nest platforms. There will be many opportunities for ospreys to exist side-by-side with humanity. We are already seeing a return of the "dooryard nests" that were common in the pre-DDT era. In many coastal areas (feeding habitat permitting), if people erect a nest platform they will get breeding ospreys.

Tolerance of man, adaptive on much of the breeding grounds, still carries great risk of mortality in certain migration and wintering areas where ospreys are shot (Colombia and Cuba, for example). A shift from tolerance of man on the breeding grounds to shyness in migration and wintering range seems to occur in areas where the birds may be persecuted (Spitzer, pers. obs.).

Now that the population has regained its reproductive power, its large potential surplus of natality over mortality will result in density-dependent pressure for adaptation to man-modified habitats. The birds can easily afford experiments in nest-site selection, and some of them, such as the nest on a 27 m light tower in the busy parking lot of a Connecticut amusement park, will be successful.

The potentially very favorable balance of natality over mortality has fascinating implications for osprey population dynamics in general:

1. It explains why Chesapeake Bay osprey populations, and some others around the world, did not suffer drastic declines during the DDT era despite moderate DDE contamination, shell thinning, and reduced hatching rates(Reese, 1977). A species which has the potential for only a relatively small rate of increase, such as the California condor (Gymnogyps californianus), would be extremely vulnerable to population decline as a result of DDR-induced reproductive failure. There is now evidence, in the form of thin eggshells and DDE in eggs, that this has been among the factors pushing the condor toward extinction (Kiff et al., 1979). The only advantage the condor has is its extreme longevite, which may allow some individuals to outlive the DDE molecules in their environment.

2. It helps to explain why ospreys can persist in areas where they periodically suffer brood-size reduction up to 50% or more, owing to food limitations, figures recorded from Florida Bay and Gardiners Island, N.Y. (Ogden, 1977; Spitzer, 1978; Poole, 1982).

3. In combination with other factors (see Spitzer, 1980), it helps account for the species' occasional high nesting density and its broad distribution throughout many parts of the world.

The osprey's unique morphology and feeding behavior, which make possible the easy exploitation of locally abundant food that is rich in energy and nutrients,play a part in permitting this favorable balance.

SUMMARY

Breeding ospreys in the coastal zone between New York City and Boston are treated as a discrete population. This region supported an estimated 1,000 active nests in the 1940's. Subsequent DDT contamination caused dramatic reproductive failure and population decline to an estimated 150 nests in 1969. Near-total annual counts of active nests and young fledged were made throughout the study period 1969-1981. Reproduction increased steadily throughout that period, coincident with declining DDT residues in eggs, and is now within the pre-DDT range. During the study period, the breeding population stopped declining and began to increase again. From a low point of 109 nests in 1976, the population increased to 168 active nests in 1981. Calculations made to examine the relationship between reproductive rate and subsequent change in population size suggest that a productivity of about 0.8 young fledged per active nest stabilized the population under the conditions which prevailed during the study period: reduced density and (presumed) age structure skewed toward older birds.

Lifs history variables such as fledging-to-breeding dispersal, site fidelity of established breeders, and age at first breeding were measured. These measurements, combined with the estimate of reproductive "break-even" point at 0.8 young per activs nest, permit estimates of annual survivorship, which appears to average at least 85% among breeders, perhaps as high as 90% in some years. The recovering population includes an increasing proportion of pairs which build a nest but do not lay eggs, apparantly the result of the increasing proportion of young inexperienced birds. The recovering population is also strongly dependent on man-made nest sites, which are being provided in abundance.

Sustained recovery of the population is predicted, because the various population parameters indicate favorable habitat conditions and a current large surplus of natality over mortality. There is great potential-already partially realized-for ospreys to breed in close association with man.

The potentially favorable balance of natality over mortality probably exists at prerent in many osprey populations and helps to explain relative stability in the face of moderate DDT contamination and the capacity of breeding ospreys to periodically sustain drastic brood-size reduction owing to food limitations. It also helps to account for the species' occasional high nesting dsnsity and broad distribution throughout many parts of the world.

ACKNOWLEDGMENTS

R e f e r e n c e s

Ames P.L. - J. Appl. Ecol., 1966, 3 (Suppl.), p. 87-97.

Ames P.L., Mersereau G.S. - Auk, 1964, 81 (2), p. 173-185.

Anderson D.R., Wywialowski A.P., Burnham K.P. - Ecology, 1981, 62 (4),
    p. 1121-1124.

Burnham K.P., Anderson D.R. - J. Wildl. Manage, 1979, 43 (2), p. 356-365.

Caughley G. Analysis of Vertebrate Populations. N.Y.: Wiley-Interscience,
    1977.

Henny C.J., Wight H.M. - Auk, 1969, 86 (2), p. 188-198.

Henny C.J., Byrd M.A., Jacobs J.A. et al. - J. Wild. Manage, 1977, 41,
    p. 254-265.

Kiff L., Peakall D., Wilbur S. - Condor, 1979, 81, p. 166-172.

Miller R.S. - Bull. of the Ecological Society of America, 1976, 57 (3), p.2-6.

Newton I. - Canadian Field-Naturalist, 1976, 90, p. 274-300.

Newton I. Population ecology of raptors. Buteo Books, Vermillion, South
    Dakota, 1979.

Ogden R. - In: Transactions of the North American osprey research conferen-
    ce / Ed. by J.C.Ogden. U.S. Nat. Park Serv., 1977, p. 143-151.

Österlöf S. - Ornis. Scand., 1977, 8, p. 61-78.

Peterson R.T. - In: Peregrine falcon populations, their biology and decline /
    Ed. by J.J.Hickey. University of Wisconsin Press, Madison, 1969, p.340-341.

Poole A. - Colonial Waterbirds, 1981, 4, p. 20-27.

Poole A. - Oecologia, 1982, 53, p. 111-119.

Puleston D. - In: Transactions of the North American osprey research confe-
    rence / Ed. by J.C.Ogden. U.S. National Park Service, 1977, p. 95-99.

Reese J.G. - Auk, 1977, 94 (2), p. 202-221.

Spitzer P.R. - In: Endangered birds: management techniques for preserving
    threatened species / Ed. by S.A.Temple. Univ. of Wisconsin Press, Madi-
    son, 1978, p. 171-182.

Spitzer P.R. Dynamics of a discrete coastal breeding population of ospreys
    in the northeastern United States during a period of decline and recovery,
    1969-1978. Unpubl. Ph. D. thesis, Cornell Univ., 1980. 90 p.

Spitzer P.R., Poole A. - Birds, 1980, 34 (3), p. 234-241.

Spitzer P.R., Risebrough R.W., Grier J.W., Sindelar C.R. Jr. - In: Trans-
    actions of the North American osprey research conference / Ed. by J.C.Og-
    den. U.S. Nat. Park Serv., 1977, p. 13-19.

Spitzer P.R., Risebrough R.W., Walker W. II et al.- Science, 1978, 202,
    p. 333-335.

Wiemeyer S.N., Spitzer P.R., Krantz W.C. et al. - J. Wildl. Manag., 1975,
    39 (1), p. 124-139.

Wilcox S.L. Banding ospreys on Long Island. N.Y. State Bulletin to the
    Schools. March, 1944. N.Y., 1944, p. 262-264.

# A SUMMARY OF RECENT AVIAN RANGE CHANGES IN EUROPE

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Long-term changes in the bird fauna or in the status of certain species have aroused great interest among ornithologists in almost every country in Europe. For some species, the population trends have been monitored over large parts of their range, even in the whole of Europe, and innumerable papers have been published on the subject. No attempt has been made, however, to analyse the changing status of all European breeding birds in a consistent manner. This is the objective of the present paper.

## MATERIAL AND METHODS

We decided not to base our analysis on published information, since it is very scattered and not easily accessible. In addition, it is based on data of very variable quality, and many of the papers are not up-to-date, Instead, we preferred to use a standard questionnaire to be sent to all European countries, except some of the smallest, such as Andorra, Luxemburg and Monaco. The form included all species breeding in Europe and was accoumpanied by a letter with instructions. For each species, the correspondent was asked to use one of the following symbols indicating its current status: I - currently increasing in range; D - currently decreasing in range ; N - no known significant change in range; ? - status unknown; - = no breeding records.

In addition, there was space for personal comments on each species (e.g. on the timing and strength of the change, and its reasons).

Replies were received from 30 countries (i.e. every country except Albania and Turkey), and also from the Estonian, Latvian and Lithuanian SSRs within the Soviet Union. In this way, we obtained up-to-date and uniform information on the entire bird fauna in Europe.

There are, however, some sources of error and shortcomings in material collected in this way. The most important ones are listed below:

1. The available information varies from species to species. The status of large, conspicuous birds (e.g. raptors, storks and swans) is particularly well known, and even slight changes in their range or number are easily observed. For small passerines, in contrast, even considerable increases or decreases may pass unnoticed unless extensive censuses are made. Hence, the results are more reliable for some species than for others.

2. The countries are of very different sizes. A change in the status of a certain species in a large country, such as France or Sweden, not to speak of the European part of the Soviet Union, is naturally more significant than a corresponding change in a small country, such as Belgium or Switzerland.

3. The information available for different countries is highly variable. Some west European countries, such as Great Britain, the Netherlands and Denmark, are ornithologically very well surveyed, with recently completed atlas studies, and the current population changes for most bird species are also well documented. In most south and east European countries, on the other hand, reliable information on the recent population trends exists for only a few species.

4. **For each country, the judgments reflect the personal view of the cor-respondent.** This means that someone else might have used different symbols for certain species, and that the practice followed in one country may have been slightly different from that in another. All countries, however, pro-vided independent assessments, so that any patterns which emerge are probably genuine.

5. **Timing of the changes has been understood in somewhat different ways by the correspondents.** The questionnaire used the term "currently" (increas-ing or decreasing), without defining more precisely how long a period should be considered. Most correspondents regarded as "current changes" those obser-ved during the last 20-30 years, while some others included only the most recent changes, taking place in the 1970s. After corrections based on the com-ments given by the correspondents and some individual queries, however, the practice followed should be fairly consistent.

6. **Changes in numbers not always taken into account.** Due to somewhat im-precise wording of the instructions, a few correspondents considered only range extensions or contractions, not changes in numbers within the range. As in the case of item 5, however, this could usually be corrected on the basis of comments on the form, or by individual queries.

The above factors have certainly affected a number of symbols used for in-dividual species in one country. What is important, however, is that they can hardly have had much effect on the general pattern for each species. Hence, we conclude that the trends which emerge from the results are, in the main, reliable, although the changes are probably mostly underestimated. In many countries, only a small part of the recent changes have so far been registe-red, and the symbol N (= no change) may in fact hide a considerable increase or large decrease. In most cases, therefore, the trends are likely to be more pronounced than revealed by the results.

The symbols were transmitted to species maps using four signs: + = increa-se, 0 = no change, - = decrease and ? = status unknown. Even changes conside-red somewhat uncertain by the correspondent (e.g. I? or D/N) were included in increases or decreases. According to the distribution of the symbols, and also considering the sizes of countries, we divided the species into seven categories. There were some border cases, as always in such classifications, but most species showed surprisingly clear patterns. Very locally distributed species occurring in only one or two countries in Europe were deleted, which left 377 species within our analysis.

## DIFFERENT PATTERNS OF CHANGES

In the following, the seven categories are treated, and a list of species and some maps presented for each.

1. **Largely no change.** The symbols 0 in clear majority. As states above, this does not mean that no trend exists, merely that no trend has been noti-ced. This is the largest category, with 134 (35.5%) species (Table 1). No less than 63.4% of them are passerines, which can hardly be due to their po-pulations being particularly stable, but rather to the fact that long-term trends are least studied for passerines. The majority of the northern wader species likewise show no significant change in their status. The reason may be that the habitats in their remote breeding regions have so far been well

Table 1. Species showing largely no change in range or numbers in Europe. The symbols indicate the status of each species in different countries (+ = increase, 0 = no change, - = decrease, ? = status unknown), the figures give the number of countries

| Species | + | 0 | - | ? |
|---|---|---|---|---|
| Podiceps grisegena | 2 | 10 | 2 | 3 |
| Calonectris diomedea | - | 5 | 1 | - |
| Puffinus puffinus | - | 8 | 2 | - |
| Hydrobates pelagicus | - | 9 | 1 | - |
| Oceanodroma leucorhoa | - | 5 | - | 1 |
| Anas penelope | - | 8 | - | 5 |
| A.acuta | 2 | 14 | 3 | 5 |
| A.clypeata | 2 | 16 | 2 | 6 |
| Mergus serrator | 1 | 13 | 1 | 1 |
| Buteo lagopus | - | 4 | - | - |
| Falco vespertinus | - | 5 | 1 | 3 |
| F.eleonorae | - | 3 | - | - |
| F.rusticolus | - | 5 | - | - |
| Lagopus mutus | - | 13 | 1 | - |
| Charadrius morinellus | - | 9 | - | 1 |
| Calidris maritima | 1 | 4 | 1 | 1 |
| C.a.alpina | - | 6 | - | - |
| Limicola falcinellus | - | 4 | - | - |
| Lymnocryptes minimus | - | 4 | 1 | 3 |
| Limosa lapponica | - | 4 | - | - |
| Numenius phaeopus | - | 7 | 2 | - |
| Tringa erythropus | - | 4 | - | - |
| T.nebularia | - | 6 | - | 2 |
| Arenaria interpres | - | 6 | - | 1 |
| Stercorarius parasiticus | - | 5 | 2 | - |
| S.longicaudus | - | 4 | - | - |
| Chlidonias hybridus | - | 8 | 1 | 4 |
| C.leucoptera | 1 | 4 | - | 3 |
| Uria lomvia | - | 3 | - | - |
| Cepphus grylle | 1 | 9 | - | - |
| Pterocles orientalis | - | 2 | - | 1 |
| Cuculus canorus | - | 21 | 4 | 2 |
| Surnia ulula | - | 4 | - | - |
| Glaucidium passerinum | - | 11 | 1 | 5 |
| Strix aluco | - | 24 | 1 | 1 |
| S.uralensis | 1 | 7 | - | 4 |
| S.nebulosa | - | 4 | - | 2 |
| Asio otus | 2 | 23 | - | 1 |
| A.flammeus | 2 | 14 | 3 | 6 |
| Aegolius funereus | - | 14 | 2 | 5 |
| Apus apus | 1 | 24 | 2 | 1 |
| A.pallidus | - | 5 | - | 1 |
| A.melba | - | 10 | - | 2 |

Table 1 (end)

| Species | + | O | − | ? |
|---|---|---|---|---|
| Picus canus | 1 | 16 | 1 | 3 |
| P.viridis | − | 21 | 1 | 2 |
| Dendrocopos major | − | 25 | − | 1 |
| D.minor | 1 | 20 | 3 | 1 |
| Picoides tridactylus | − | 11 | 3 | 4 |
| Calandrella brachydactyla | − | 8 | 1 | 1 |
| Galerida theklae | − | 2 | − | 1 |
| Eremophila alpestris | − | 5 | 1 | 1 |
| Hirundo rupestris | − | 9 | − | 2 |
| Delichon urbica | 3 | 23 | 1 | 2 |
| Anthus trivialis | − | 23 | − | 4 |
| A. cervinus | − | 4 | − | − |
| A.spinoletta | 1 | 17 | − | 2 |
| Motacilla alba | − | 27 | 1 | 1 |
| Bombycilla garrulus | − | 4 | − | − |
| Troglodytes troglodytes | − | 26 | 1 | 1 |
| Prunella modularis | 3 | 21 | − | 3 |
| P.collaris | − | 13 | − | 1 |
| Cercotrichas galactotes | − | 3 | − | 1 |
| Erithacus rubecula | 1 | 25 | 1 | 1 |
| Luscinia megarhynchos | 2 | 13 | 3 | 1 |
| Saxicola torquata | 2 | 14 | 2 | 3 |
| Oenanthe pleschanka | − | 3 | − | − |
| Oe.hispanica | − | 5 | − | 3 |
| Monticola solitarius | 1 | 6 | 1 | 2 |
| Turdus torquatus | 1 | 16 | 1 | 1 |
| T. philomelos | 2 | 24 | − | − |
| T.viscivorus | − | 24 | 2 | 1 |
| Acrocephalus melanopogon | − | 7 | 1 | 2 |
| Hippolais pallida | 1 | 4 | − | 1 |
| H. icterina | − | 18 | 2 | 2 |
| H.polyglotta | 1 | 4 | − | 2 |
| Sylvia sarda | − | 3 | − | − |
| S.undata | − | 4 | − | 1 |
| S.conspicillata | − | 4 | − | 1 |
| S.cantillans | − | 5 | − | 2 |
| S.melanocephala | − | 6 | − | 3 |
| S.hortensis | − | 5 | 1 | 2 |
| S.curruca | 1 | 21 | 1 | − |
| S.borin | − | 22 | − | 5 |
| S.atricapilla | 1 | 23 | − | 3 |
| Phylloscopus borealis | − | 4 | − | − |
| Ph.bonelli | − | 9 | 1 | 2 |
| Ph.sibilatrix | 1 | 20 | 1 | 2 |
| Ph.collybita | 1 | 24 | − | 2 |
| Ph.trochilus | 1 | 19 | − | 2 |
| Regulus regulus | 1 | 22 | 1 | 2 |

preserved, but lack of information may also play a part. Some characteristic representatives of this category are shown in Fig. 1.

2. No change or decreasing. Roughly 20-50% of the symbols indicating decrease, the rest mainly no change. The second largest category, comprising 91 (24.1%) species (Table 2). The range of the area with a decreasing trend varies from species to species, but some consistent patterns are repeated strikingly often. Several species show a decrease only in the nucleus of their range, in central Europe, but are fairly stable in the more peripheral areas (e.g. Tetrao tetrix, Rallus aquaticus, Scolopax rusticola, Actitis hypoleucos, Alauda arvensis, Hirundo rustica, Anthus campestris,Sylvia communis). Another pattern, common to still more species, shows a decreasing trend in the western and central parts of Europe, but no significant change in the rest of the range (e.g. Botaurus stellaris, Ixobrychus minutus, Anas querquedula, Bonasa bonasia, Burhinus oedicnemus, Charadrius alexandrinus, Gallinago gallinago, Tringa totanus, Alcedo atthis, Luscinia svecica, Saxicola rubertra, Lanius collurio, L.minor, L.senator, Emberiza hortulana). In some species,decreases are reported from considerable parts of the range (e.g. Sterna hirundo, Chlidonias niger, Caprimulgus europaeus, Upupa epops, Galerida cristata, Lullula arborea, Phoenicurus phoenicurus). Fig. 2 gives some examples of these patterns.

3. No change or increasing. Rougly 20-50% of the symbols indicating an increase, the rest mainly no change. Clearly smaller than the previous category, with 47 (12.5%) species (Table 3). The most conspicuous pattern is shown by species increasing and expanding in the northern parts of their range, but having fairly stable populations elsewhere (e.g. Ardea cinerea, Circus aeruginosus, Gallinula chloropus, Recurvirostra avosetta, Columba palumbus, Phoenicurus ochruros, Locustella luscinioides, Acrocephalus palustris, Panurus biarmicus, Serinus serinus). Some species show increases over considerable parts of their range (e.g. Podiceps cristatus, Anas strepera, Aythya ferina, Buteo buteo, Fulica atra, Vanellus vanellus, Turdus merula, Pica pica). Fig.3 depicts some species showing different patterns of increase.

4. Decreasing in some parts, increasing in others. Both decreasing and increasing trends evident in some parts of the range, on change in the rest of area. Almost as large as the last category with 44 (11.7%) species (Table 4). Many of them show the same pattern, increasing and expanding in the north, but simultaneously decreasing in western and/or central Europe (e.g. Circus pygargus, Charadrius dubius, Philomachus pugnax, Limosa limosa, Sterna paradisaea, Streptopelia turtur, Motacilla cinerea, Locustella naevia, L.fluviatilis, Acrocephalus scirpaceus, A.arundinaceus, Sylvia nisoria, Lanius excubitor). A few species are on the increase, at least locally, in the western parts of their range, while decreasing in the east (e.g. Phalacrocorax carbo , Ph. aristotelis, Milvus milvus, Accipiter gentilis, A.nisus). An opposite trend, increase in eastern Europe, but decrease in most other parts of the range, is shown by Gypaetus barbatus, Neophron percnopterus and Tetrax tetrax. Exceptional patterns emerge from the maps of Ciconia nigra (decrease in SW and NE, increase in some central European countries), Milvus migrans (decrease in the central parts of the range, increase in both W and E) and Larus fuscus (decrease in N, increase in W and SW). Most of the remaining species show a

Table 2. Species either decreasing or showing no change in range or numbers in Europe. For explanations, see Table 1

| Species | + | 0 | − | ? |
|---|---|---|---|---|
| Podiceps nigricollis | 2 | 10 | 7 | 3 |
| Botaurus stellaris | 1 | 11 | 10 | 1 |
| Ixobrychus minutus | − | 8 | 5 | 3 |
| Ardea purpurea | 1 | 8 | 5 | 3 |
| Platalea leucorodia | 1 | 4 | 4 | − |
| Anser fabalis | − | 2 | 2 | − |
| Tadorna ferruginea | − | 2 | 3 | 1 |
| Anas crecca | − | 15 | 8 | 3 |
| A.querquedula | 1 | 15 | 8 | 1 |
| Aythya nyroca | − | 9 | 5 | 2 |
| A.marila | − | 4 | 3 | 1 |
| Clangula hyemalis | − | 3 | 1 | 1 |
| Melanitta nigra | − | 5 | 2 | 1 |
| M.fusca | − | 2 | 2 | − |
| Pernis apivorus | − | 14 | 6 | 6 |
| Circaetus gallicus | − | 5 | 6 | 4 |
| Accipiter brevipes | − | 2 | 1 | 1 |
| Aquila pomarina | 1 | 7 | 3 | − |
| A.chrysaetos | 2 | 8 | 9 | − |
| Hieraetus pennatus | − | 6 | 3 | 1 |
| H.fasciatus | − | 2 | 2 | 1 |
| Pandion haliaetus | 2 | 5 | 7 | 2 |
| Falco naumanni | − | 3 | 6 | 4 |
| F.tinnunculus | − | 20 | 7 | 1 |
| F.subbuteo | − | 13 | 10 | 2 |
| F.biarmicus | − | 1 | 1 | 1 |
| F.cherrug | − | 3 | 3 | − |
| Bonasa bonasia | − | 8 | 7 | 4 |
| Lagopus lagopus | − | 4 | 4 | − |
| Tetrao tetrix | − | 10 | 11 | 1 |
| Alectoris chucar | − | 2 | 1 | 2 |
| A.rufinus | − | 2 | 3 | 1 |
| Rallus aquaticus | 1 | 17 | 5 | 6 |
| Porzana porzana | − | 11 | 5 | 8 |
| Porphyrio porphyrio | − | 1 | 2 | − |
| Grus grus | − | 7 | 5 | − |
| Burhinus oedicnemus | − | 7 | 5 | 3 |
| Glareola pratincola | − | 5 | 2 | 2 |
| Charadrius hiaticula | − | 11 | 7 | 1 |
| C.alexandrinus | − | 10 | 6 | 1 |
| Pluvialis apricaria | 1 | 5 | 6 | 4 |
| Gallinago gallinago | − | 11 | 11 | 3 |
| Scolopax rusticola | 2 | 12 | 7 | 3 |
| Numenius arquata | 2 | 11 | 9 | − |

10. Зак. 981

Table 2 (continued)

| Species | + | ○ | − | ? |
|---|---|---|---|---|
| Tringa totanus | 2 | 14 | 10 | − |
| Actitis hypoleucos | − | 16 | 5 | 4 |
| Larux audouinii | − | 2 | 2 | − |
| Gelochelidon nilotica | − | 5 | 2 | 2 |
| Sterna hirundo | 1 | 14 | 11 | − |
| Chlidonias niger | − | 8 | 11 | 4 |
| Uria aalge | 1 | 7 | 5 | − |
| Alca torda | − | 6 | 3 | − |
| Fratercula arctica | − | 5 | 2 | − |
| Pterocles alchata | − | 2 | 1 | − |
| Otus scops | − | 6 | 6 | 2 |
| Nyctea scandiaca | − | 2 | 2 | 2 |
| Caprimulgus europaeus | − | 9 | 13 | 5 |
| Alcedo atthis | 3 | 10 | 12 | 2 |
| Upupa epops | − | 8 | 11 | 3 |
| Merops apiaster | − | 9 | 3 | 2 |
| Iynx torquilla | − | 16 | 8 | 1 |
| Dendrocopos medius | − | 12 | 5 | 3 |
| D.leucotos | − | 11 | 6 | 2 |
| Melanocorypha calandra | − | 5 | 2 | 1 |
| Galerida cristata | 1 | 10 | 10 | 2 |
| Lullula arborea | − | 11 | 13 | 2 |
| Alauda arvensis | − | 18 | 8 | 2 |
| Riparia riparia | 1 | 19 | 5 | 2 |
| Hirundo rustica | 1 | 19 | 8 | 1 |
| Anthus campestris | 1 | 14 | 5 | 3 |
| Motacilla flava | 3 | 14 | 8 | 1 |
| Cinclus cinclus | 1 | 15 | 6 | 2 |
| Luscinia svecica | 1 | 9 | 6 | 3 |
| Phoenicurus phoenicurus | − | 15 | 10 | 2 |
| Saxicola rubetra | − | 16 | 10 | − |
| Oenanthe oenanthe | − | 22 | 6 | 1 |
| Oe.leucura | − | 1 | 1 | 1 |
| Monticola saxatilis | − | 10 | 3 | 1 |
| Acrocephalus paludicola | − | 4 | 3 | 4 |
| A.schoenobaenus | 2 | 14 | 8 | − |
| Sylvia communis | − | 18 | 7 | 2 |
| Parus cinctus | − | 2 | 2 | − |
| Lanius collurio | 1 | 12 | 12 | 1 |
| L.minor | − | 8 | 7 | 1 |
| L.senator | − | 6 | 8 | 3 |
| Perisoreus infaustus | − | 3 | 1 | − |
| Pinicola enucleator | − | 3 | 1 | − |
| Emberiza citrinella | − | 20 | 6 | 1 |
| E.cirlus | − | 6 | 2 | 4 |

Table 2  (end)

| Species | + | O | − | ? |
|---|---|---|---|---|
| E.hortulana | − | 11 | 10 | 2 |
| Miliaria calandra | 2 | 8 | 11 | 3 |
| R.ignicapillus | 3 | 14 | − | 3 |
| Muscicapa striata | − | 24 | 2 | 2 |
| Picedula parva | 1 | 8 | 1 | 5 |
| Aegithalos caudatus | 1 | 23 | 1 | 2 |
| Parus palustris | 1 | 19 | 2 | 1 |
| P.lugubris | − | 4 | − | 1 |
| P.montanus | − | 18 | 1 | 4 |
| P.cristatus | 1 | 21 | 2 | 2 |
| P.ater | 1 | 22 | 1 | 3 |
| P.caeruleus | 1 | 25 | − | 1 |
| P.major | 4 | 21 | − | 2 |
| Sitta europaea | 1 | 21 | − | 3 |
| S.neumayer | − | 3 | − | − |
| Tichodroma muraria | − | 11 | 1 | 1 |
| Certhia familiaris | − | 21 | − | 5 |
| C.brachydactyla | 1 | 14 | − | 3 |
| Oriolus oriolus | 2 | 19 | 1 | 3 |
| Garrulus glandarius | 4 | 20 | − | 2 |
| Nucifraga caryocatactes | 3 | 14 | − | 4 |
| Pyrrhocorax graculus | 2 | 8 | − | − |
| P.pyrrhocorax | 1 | 6 | 1 | 3 |
| Corvus monedula | 4 | 19 | 3 | 2 |
| C.corone | 3 | 21 | 1 | 3 |
| Passer domesticus | 1 | 25 | 1 | 2 |
| P.montanus | 1 | 21 | 3 | 1 |
| Petronia petronia | 1 | 5 | − | 2 |
| Montifringilla nivalis | 1 | 6 | 1 | − |
| Fringilla coelebs | 1 | 26 | − | − |
| F.montifringilla | 1 | 4 | 1 | 4 |
| Serinus citrinella | − | 6 | − | 1 |
| Carduelis chloris | 2 | 23 | − | 2 |
| C.carduelis | 3 | 21 | − | 2 |
| C.spinus | 3 | 18 | − | 4 |
| C.cannabina | 2 | 22 | 2 | 2 |
| C.flavirostris | − | 4 | − | 1 |
| Loxia leucoptera | − | 3 | − | − |
| L.curvirostra | 2 | 19 | 1 | 5 |
| L.pytyopsittacus | − | 5 | − | 3 |
| Pyrrhula pyrrhula | − | 24 | − | 2 |
| Coccothraustes coccothraustes | 2 | 21 | − | 3 |
| Calcarius lapponicus | 1 | 4 | − | − |
| Plectrophenax nivalis | − | 6 | − | − |
| Emberiza cia | 1 | 10 | 2 | 1 |
| E.melanocephala | − | 4 | − | 2 |

T a b l e 3. Species either increasing or showing no change in range or numbers in Europe.For explanations, see Table 2

| Species | + | 0 | - | ? |
|---|---|---|---|---|
| Tachybaptus ruficollis | 5 | 17 | 1 | - |
| Podiceps cristatus | 13 | 13 | - | 1 |
| P.auritus | 2 | 5 | - | 3 |
| Ardeola ralloides | 3 | 5 | 1 | 1 |
| Egretta garzetta | 4 | 4 | 1 | 2 |
| Ardea cinerea | 13 | 11 | 2 | 1 |
| Phoenicopterus ruber | 1 | 2 | - | - |
| Branta leucopsis | 2 | 2 | - | - |
| Anas strepera | 13 | 10 | 1 | 3 |
| A.platyrhynchos | 6 | 20 | 2 | 1 |
| Netta rufina | 4 | 8 | 1 | 3 |
| Aythya ferina | 13 | 13 | - | 2 |
| Bucephala clangula | 5 | 6 | 1 | - |
| Mergus albellus | 1 | 2 | - | 1 |
| Circus aeruginosus | 11 | 10 | 2 | 2 |
| Buteo buteo | 9 | 17 | - | 1 |
| Gallinula chloropus | 5 | 21 | 1 | - |
| Fulica atra | 10 | 17 | - | 1 |
| Haematopus ostralegus | 8 | 10 | 2 | 1 |
| Recurvirostra avosetta | 8 | 8 | 3 | 1 |
| Vanellus vanellus | 12 | 12 | 3 | 1 |
| Tringa stagnatilis | 1 | 2 | - | 1 |
| T.ochropus | 4 | 6 | 2 | 2 |
| Larus melanocephalus | 4 | 9 | 1 | - |
| L.genei | 2 | 1 | 1 | 1 |
| Sterna caspia | 2 | 3 | - | 2 |
| Columba palumbus | 7 | 21 | - | 1 |
| Dendrocopos syriacus | 4 | 5 | - | - |
| Hirundo daurica | 3 | 2 | - | 3 |
| Luscinia luscinia | 5 | 5 | 2 | 1 |
| Tarsiger cyanurus | 2 | 1 | - | - |
| Phoenicurus ochruros | 9 | 15 | 1 | 1 |
| Turdus merula | 12 | 16 | - | 1 |
| Locustella luscinioides | 8 | 11 | 1 | 4 |
| Acrocephalus agricola | 1 | 1 | - | 1 |
| A.palustris | 5 | 18 | 1 | - |
| Ficedula albicollis | 3 | 9 | - | 2 |
| F.hypoleuca | 5 | 14 | - | 2 |
| Panurus biarmicus | 9 | 6 | 3 | 3 |
| Remiz pendulinus | 6 | 10 | 1 | 3 |
| Pica pica | 6 | 19 | 1 | 1 |
| Sturnus vulgaris | 7 | 19 | 1 | 1 |
| S.unicolor | 1 | 2 | - | 1 |
| Passer hispaniolensis | 3 | 4 | 1 | - |

Table 4. Species decreasing in some parts of Europe and increasing in others. For explanations, see Table 1

| Species | + | 0 | - | ? |
|---|---|---|---|---|
| Phalacrocorax carbo | 4 | 9 | 5 | 1 |
| Ph.aristotelis | 3 | 8 | 1 | - |
| Ph.pygmaeus | 1 | 1 | 3 | - |
| Nycticorax nycticorax | 3 | 7 | 2 | 4 |
| Egretta alba | 3 | 2 | 3 | 1 |
| Ciconia nigra | 4 | 8 | 5 | - |
| Plegadis falcinellus | 1 | 2 | 1 | 1 |
| Mergus merganser | 4 | 10 | 4 | - |
| Milvus migrans | 4 | 7 | 7 | 3 |
| M.milvus | 5 | 5 | 6 | 4 |
| Gypaetus barbatus | 1 | 2 | 3 | - |
| Neophron percnopterus | 1 | 1 | 4 | 2 |
| Circus cyaneus | 2 | 10 | 4 | 4 |
| C.pygargus | 2 | 9 | 6 | 5 |
| Accipiter gentilis | 6 | 5 | 13 | 2 |
| A.nisus | 5 | 9 | 11 | 2 |
| Buteo rufinus | 1 | 1 | 1 | - |
| Phasianus colchicus | 9 | 9 | 3 | 3 |
| Tetrax tetrax | 1 | 2 | 3 | 2 |
| Himanthopus himanthopus | 2 | 7 | 3 | - |
| Charadrius dubius | 6 | 13 | 5 | 2 |
| Calidris temminckii | 1 | 2 | 2 | - |
| Philomachua pugnax | 3 | 4 | 8 | - |
| Limosa limosa | 5 | 4 | 10 | 1 |
| Tringa glareola | 1 | 5 | 3 | 4 |
| Phalaropus lobatus | 1 | 6 | 2 | - |
| Stercorarius skua | 1 | 1 | 1 | 1 |
| Larus minutus | 3 | 6 | 2 | 1 |
| L.fuscus | 6 | 6 | 3 | - |
| Sterna sandvicensis | 3 | 7 | 2 | - |
| S.paradisaea | 4 | 8 | 4 | - |
| Columba livia | 2 | 11 | 4 | - |
| Streptopelia turtur | 4 | 14 | 4 | 3 |
| Dryocopus martius | 5 | 15 | 2 | 2 |
| Anthus pratensis | 2 | 13 | 6 | 2 |
| Motacilla cinerea | 5 | 14 | 3 | 2 |
| Locustella naevia | 5 | 11 | 4 | 4 |
| L.fluviatilis | 4 | 4 | 3 | 4 |
| Acrocephalus scirpaceus | 5 | 16 | 3 | 2 |
| A.arundinaceus | 3 | 11 | 8 | 2 |
| Sylvia nisoria | 2 | 10 | 3 | 3 |
| Lanius excubitor | 4 | 6 | 9 | 2 |
| Corvus frugilegus | 8 | 12 | 5 | - |
| Emberiza schoeniclus | 5 | 17 | 3 | 1 |
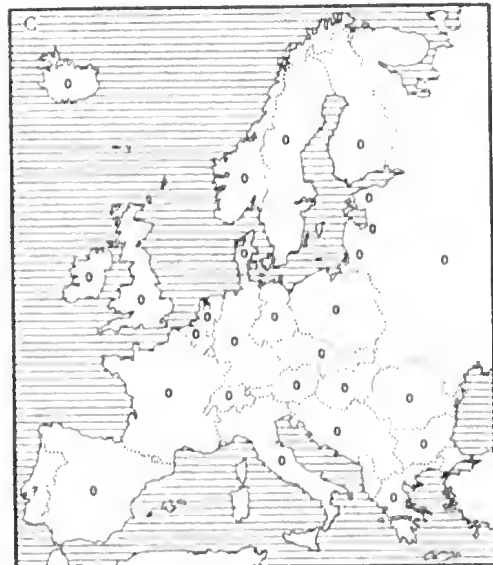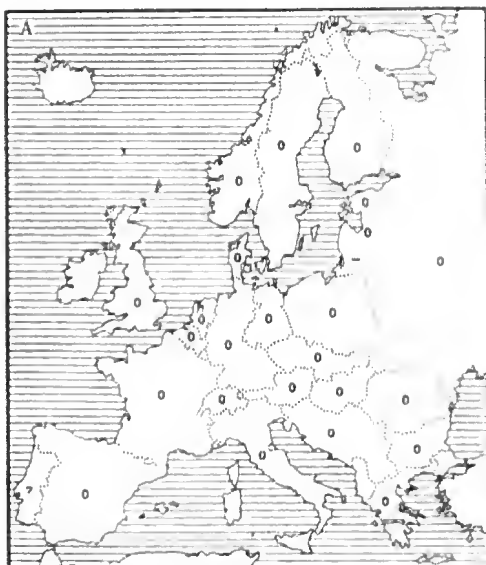
F i g. 1. Species showing largely no change in range or numbers in Europe
A – <u>Strix aluco</u>; B – <u>Apus melba</u>; C – <u>Motacilla alba</u>; D – <u>Plectrophenax</u>
<u>nivalis</u>; + – increase, O – no change, – – decrease, ? – status unknown

mosaic-like distribution of + and – symbols, indicating that local changes
in the availability of habitats or conservation measures have affected their
status (e.g. <u>Nycticorax nycticorax</u>, <u>Egretta alba</u>, <u>Mergus merganser</u>, <u>Himantho-</u>
<u>pus himanthopus</u>, <u>Corvus frugilegus</u>). Fig. 4 shows some typical representati-
ves of these different patterns.

　　Largely decreasing. More than half of the symbols indicating a decrease,
Twentynine species or 7.7% belong to this category, which is especially im-
portant with respect to nature conservation (Table 5, Fig. 5). About half of
them are widely distributed in Europe and have decreased in an alarming man-
726
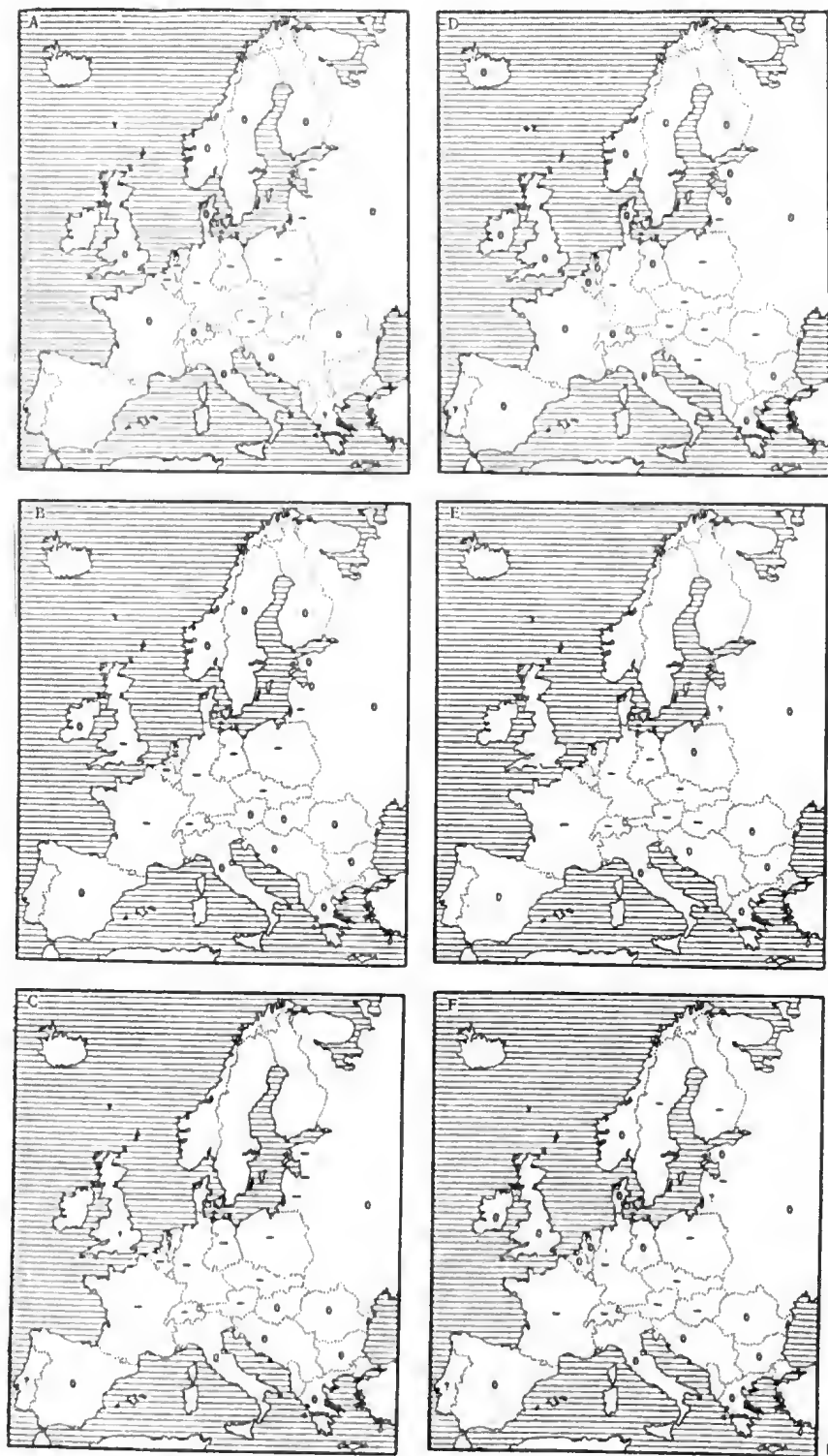
F i g. 2. Species showing no change or decreasing in Europe. Cf. Fig. 1
    A - Tetrao tetrix; B - Saxicola rubetra; C - Upupa epops; D - Hirundo
rustica; E - Lanius minor; F - Phoenicurus phoenicurus
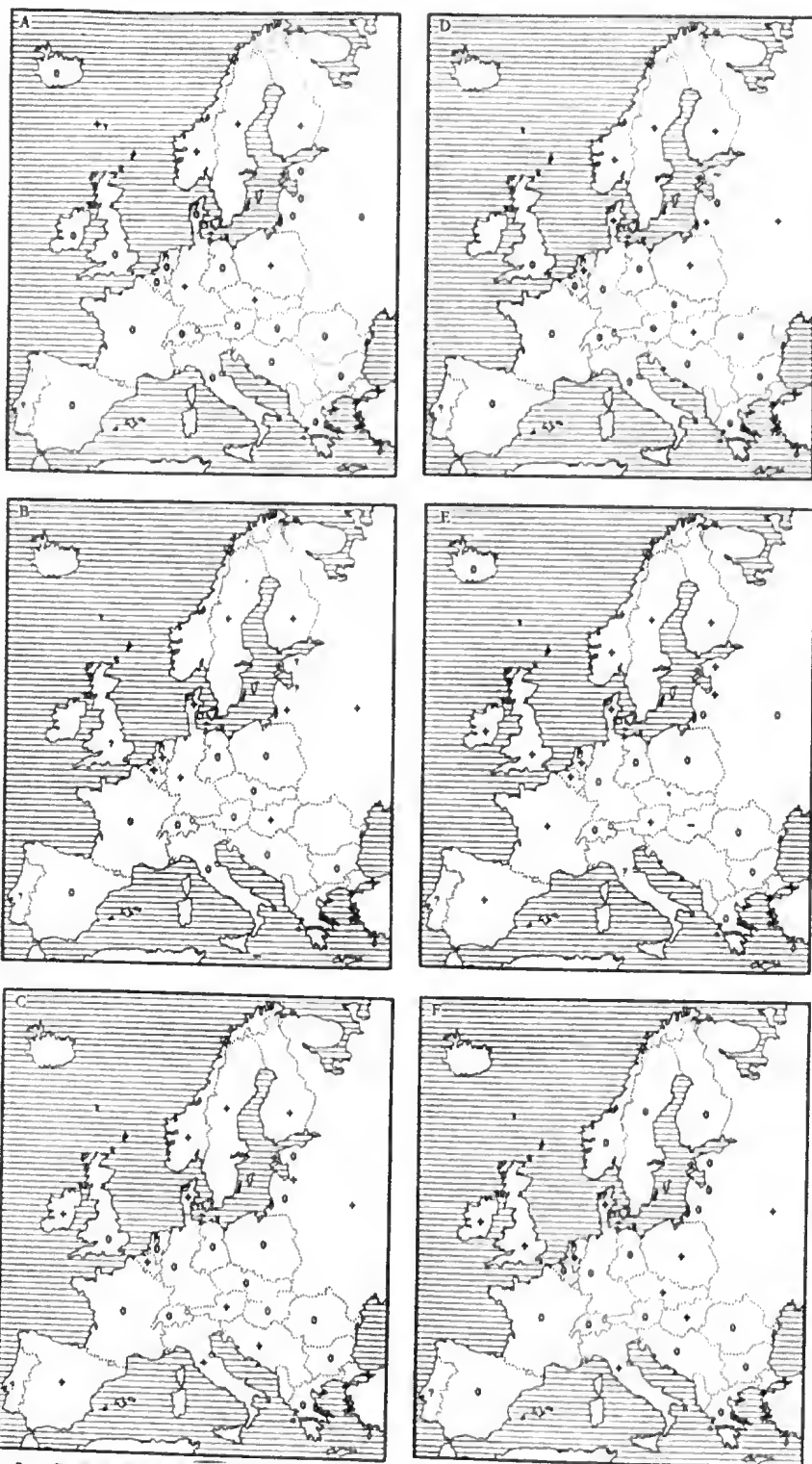
F i g. 3. Species showing no change or increasing in Europe. Cf. Fig. 1
A - <u>Columba palumbus</u>; B - <u>Serinus serinus</u>; C - <u>Podiceps cristatus</u>; D -
<u>Phoenicurus ochruros</u>; E - <u>Anas strepera</u>; F - <u>Buteo buteo</u>

728
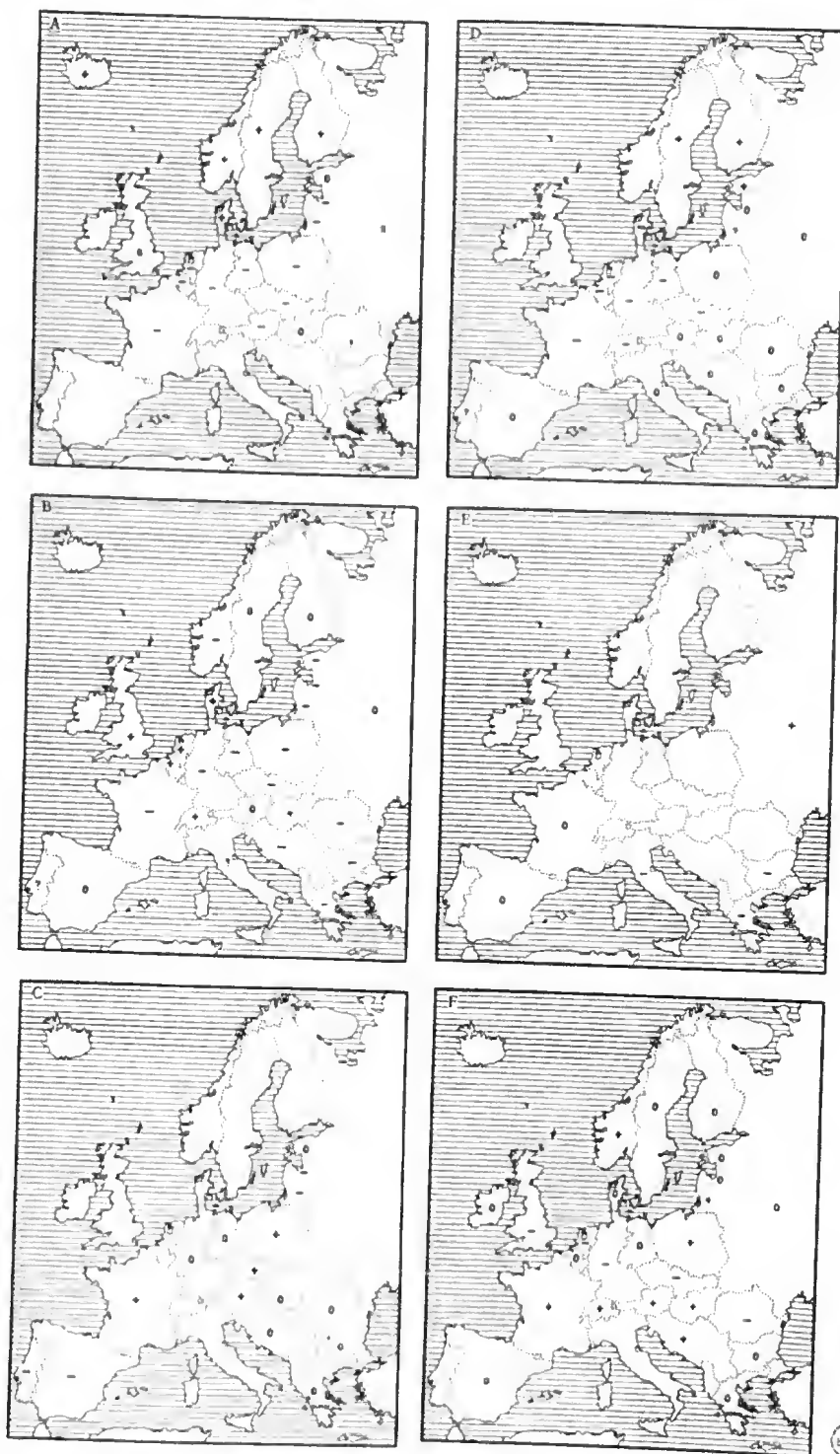
F i g. 4. Species decreasing in some parts of Europe and increasing in :: : others. Cf. Fig. 1

A – <u>Limosa limosa</u>; B – <u>Accipiter gentilis</u>; C – <u>Ciconia nigra</u>; D – <u>Acro-cephalus arundinaceus</u>; E – <u>Gypaetus barbatus</u>; F – <u>Corvus frugilegus</u>
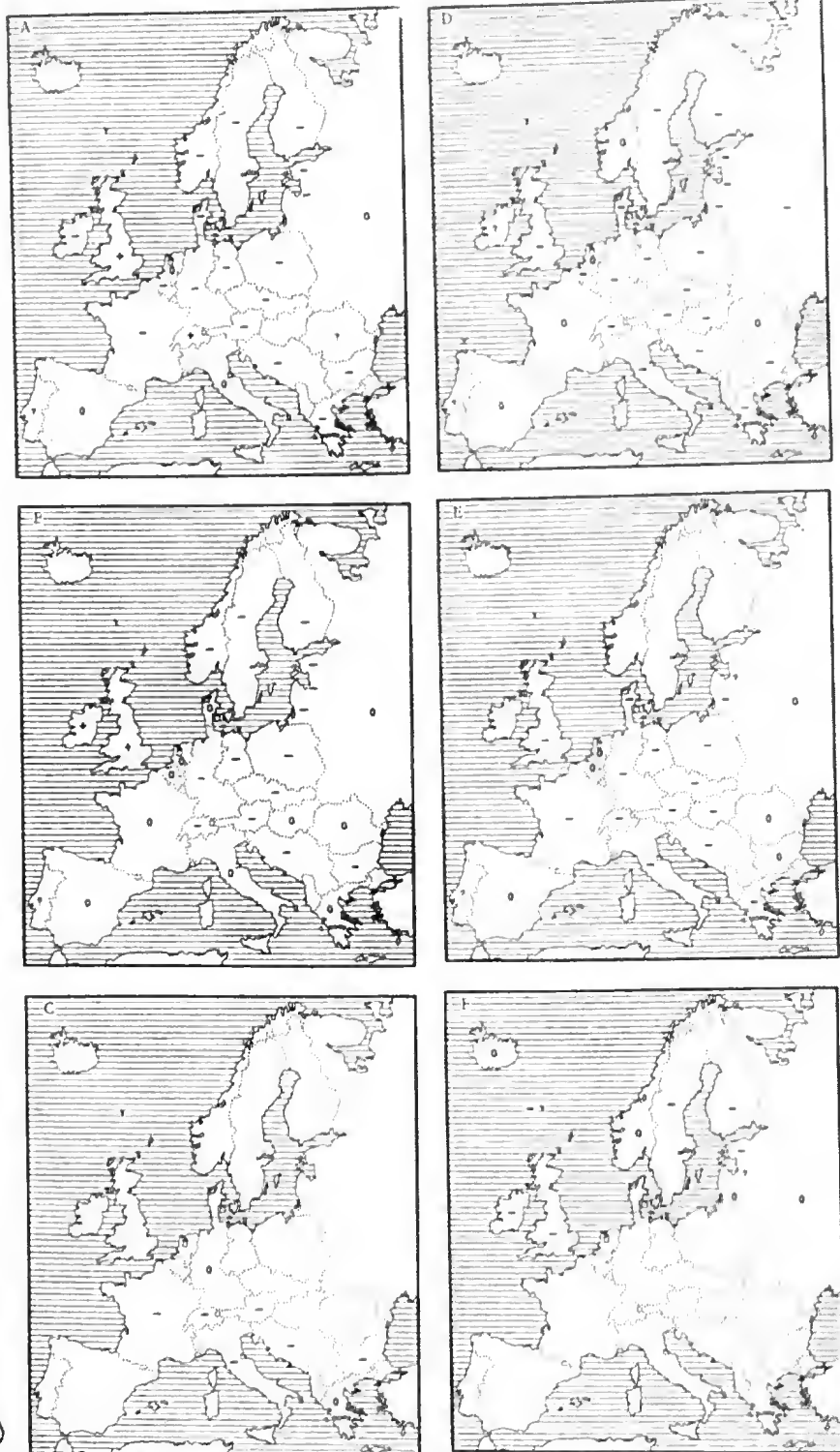
F i g. 5. Largely decreasing species in Europe. Cf. Fig. 1

A - Falco peregirinus; B - Columba oenas; C - Alectoris graeca; D - Per-
dix perdix; E - Athene noctua; F - Falco columbarius
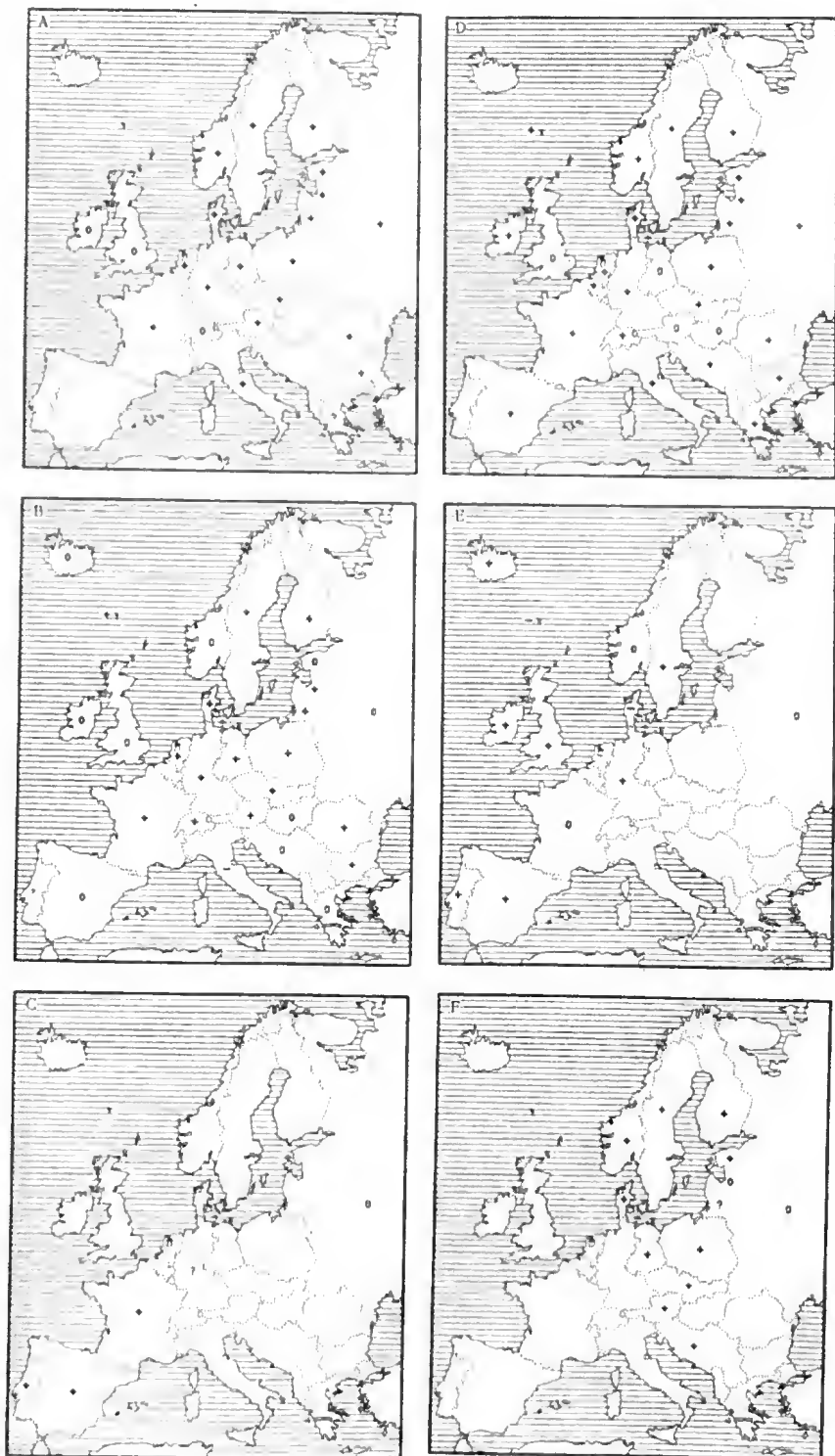
F i g. 6. Largely increasing species in Europe. Cf. Fig. 1
A - Cygnus olor; B - Corvus corax; C - Bubulcus ibis; D - Streptopelia
decaocto; E - Rissa tridactyla; F - Carpodacus erythrinus

T a b l e  5. Species largely decreasing in range or numbers in Europe. For explanations, see Table 1

| Species | + | O | – | ? |
|---|---|---|---|---|
| Gavia stellata | – | 4 | 5 | – |
| G. arctica | – | 4 | 5 | – |
| Pelecanus onocrotalus | – | – | 4 | – |
| P. crispus | – | 1 | 3 | – |
| Ciconia ciconia | 2 | 7 | 10 | – |
| Anser erythropus | – | 1 | 3 | – |
| Marmaronetta angustirostris | – | – | 2 | 1 |
| Oxyura leucocephala | – | – | 3 | – |
| Haliaeetus albicilla | 1 | 4 | 9 | – |
| Gyps fulvus | 1 | – | 6 | – |
| Aegypius monachus | – | 1 | 3 | 1 |
| Aquila heliáca | – | 1 | 7 | – |
| Falco columbarius | – | 4 | 6 | 1 |
| F. peregrinus | 2 | 5 | 17 | 2 |
| Tetrao urogallus | – | 5 | 15 | 1 |
| Alectoris graeca | – | 2 | 6 | – |
| Perdix perdix | – | 5 | 20 | 2 |
| Coturnix coturnix | – | 6 | 18 | 2 |
| Crex crex | – | 4 | 19 | 2 |
| Otis tarda | 1 | – | 9 | 1 |
| Calidris alpina schinzii | – | 3 | 7 | 2 |
| Gallinago media | – | 1 | 7 | 1 |
| Sterna dougallii | – | – | 3 | – |
| S. albifrons | 2 | 6 | 14 | 1 |
| Columba oenas | 2 | 10 | 14 | 1 |
| Tyto alba | 1 | 8 | 14 | 2 |
| Bubo bubo | 2 | 4 | 15 | 1 |
| Athene noctua | – | 6 | 14 | 2 |
| Coracias garrulus | – | 7 | 9 | 1 |

ner in most parts of the range in recent time (e.g. Ciconia ciconia, Falco peregrinus, Tetrao urogallus, Perdix perdix, Coturnix coturnix, Crex crex, Sterna albifrons, Columba oenas, Bubo bubo, Athene noctua). The rest include both southern (e.g. Oxyura leucocephala, Alectoris graeca) and nothern species (e.g. Gavia stellata, Anser erythropus, Falco columbarius), and western (Calidris alpina schinzii, Sterna dougallii) and eastern species as well (Pelecanus onocrotalus, P. crispus), some of which having a very restricted distribution in Europe.

6. Largely increasing. More than half the symbols indicate an increase. Of these 26 species (6.9%) about one half is widely distributed (e.g. Cygnus olor. Anser anser, Larus ridibundus, Streptopelia decaocto, Turdus pilaris, Corvus corax), five are oceanic (Fulmarus glacialis, Sula bassana, Somateria mollissima, Larus marinus, Rissa tridactyla), four southern (Bubulcus ibis, Cettia cetti, Cisticola juncidis, Estrilda astrild) three northern (Cygnus

T a b l e  6. Species largely increasing in range or numbers
in Europe. For explanations, see Table 1

| Species | + | 0 | - | ? |
|---------|---|---|---|---|
| Fulmarus glacialis | 5 | 3 | - | - |
| Sula bassana | 4 | 2 | - | - |
| Bubulcus ibis | 3 | 1 | - | 1 |
| Cygnus olor | 18 | 3 | - | 1 |
| C.cygnus | 4 | 1 | - | 2 |
| Anser anser | 16 | 2 | 3 | 1 |
| Branta canadensis | 6 | - | - | 1 |
| Tadorna tadorna | 13 | 8 | - | - |
| Aythya fuligula | 14 | 6 | 1 | 2 |
| Somateria mollissima | 8 | 4 | 1 | 1 |
| Larus ridibundus | 19 | 7 | 1 | - |
| L.canus | 12 | 7 | 1 | - |
| L.argentatus | 18 | 6 | 2 | - |
| L.marinus | 6 | 4 | 1 | - |
| Rissa tridactyla | 7 | 3 | 2 | - |
| Streptopelia decaocto | 23 | 4 | - | - |
| Turdus pilaris | 13 | 6 | 2 | 1 |
| T.iliacus | 8 | 5 | - | 1 |
| Cettia cetti | 9 | 4 | - | 1 |
| Cisticola juncidis | 6 | 3 | - | 1 |
| Acrocephalus dumetorum | 4 | 1 | - | 1 |
| Corvus corax | 16 | 10 | 1 | 1 |
| Estrilda astrild | 2 | - | - | 1 |
| Carduelis flammea | 11 | 7 | - | - |
| Carpodacus erythrinus | 10 | 2 | - | 1 |
| Emberiza rustica | 3 | 1 | - | 1 |

cygnus, Branta canadensis, Turdus iliacus) and two eastern (Acrocephalus du-
metorum, Carpodacus erythrinus). See Table 6 and Fig. 6.

.7. Status largely unknown. About half the symbols are question-marks. In
addition to species for which the available information was insufficient,
question-marks were also used for species not breeding regularly in the count-
ry or fluctuating in numbers. Only six species or 1.6% belong to this catego-
ry, most of them having a restricted distribution and low numbers in Europe
(Table 7).


TRENDS IN DIFFERENT ORDERS

Talbe 8 shows the proportions of decreasing and increasing species in or-
ders with at least four species. In this analysis, the above categories 2 and
5 (decreasing) and categories 3 and 6 (increasing) are combined, while catego-
ries 1,4 and 7 have been deleted.

The alarming situation of the raptors in Europe, stressed by the nature
conservationists in many countries, is evident from this material also: more

T a b l e  7. Species whose status in Europe is largely unknown. For explanations, see Table 1

| Species | + | 0 | - | ? |
|---------|---|---|---|---|
| Aix galericulata | - | 2 | - | 3 |
| Aquila clanga | - | 3 | 1 | 4 |
| Porzana parva | - | 8 | 2 | 9 |
| P.pusilla | - | 5 | 1 | 7 |
| Calandrella rufescens | - | 2 | - | 2 |
| Phylloscopus trochiloides | - | 3 | - | 5 |

than half the species show a general decrease and only two (Buteo buteo, Circus aeruginosus) are on the increase. Still more alarming is the status of gallinaceous birds: no less than 9 of the 11 species are declining, many of them drastically, and not a single species shows the opposite trend. The members of this group represent birds of widely different habitats and different ecologies, which makes their general decline difficult to explain.The marked decrease of all the four species of Coraciiformes is also remarkable, as well as the high proportion of decreasing species among cranes, rails and bustards (Gruiformes), waders, gulls and auks (Charadriiformes) and owls (Strigiformes). On the whole, the number of decreasing species exceeds that of increasing species in most orders, which gives a rather depressing picture of the future for European birds.

T a b l e  8. Proportions of decreasing species in different orders (only orders with four or more species are included)

| Order | N of species | Per cent | |
|-------|------|------------|------------|
| | | decreasing | increasing |
| Podicipediformes | 5 | 20.0 | 60.0 |
| Procellariiformes | 5 | - | 20.0 |
| Pelecaniiformes | 6 | 33.3 | 16.7 |
| Ciconiiformes | 14 | 35.7 | 35.7 |
| Anseriformes | 31 | 38.7 | 45.2 |
| Falconiformes | 35 | 54.3 | 5.7 |
| Galliformes | 11 | 81.8 | - |
| Gruiformes | 11 | 54.5 | 18.2 |
| Charadriiformes | 62 | 33.9 | 21.0 |
| Columbiformes | 7 | 28.6 | 28.6 |
| Strigiformes | 13 | 38.5 | - |
| Coraciiformes | 4 | 100.0 | - |
| Piciformes | 10 | 30.0 | 10.0 |
| Passeriformes | 155 | 18.1 | 18.7 |

REGIONAL TRENDS

Europe can be divided into four quarters, northern, western, southern and eastern, with 7 to 9 countries in each (Fig. 7). The proportions of symbols within these quarters give a rough picture of the regional trends in avian
734
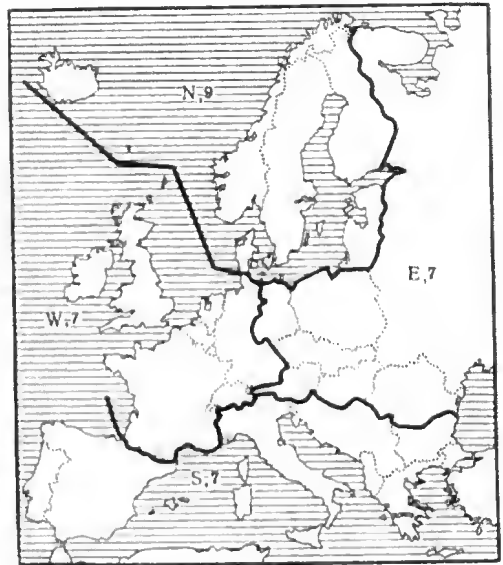
F i g. 7. The four quarters of Europe used for an analysis of the regional trends in avian range changes

range changes in Europe. Table 9 summarizes the results of such an analysis.

The following two general conclusions can be drawn. First, only in northern Europe does the number of increasing species equal that of decreasing birds. In other parts of Europe the decreases predominate, this being most pronounced in the southern and eastern quarters. Secondly, the proportions of symbols ( and ? are much higher in southern and eastern than in northern and western Europe, amounting together to 70-80%. The explanation can hardly be that bird populations are more stable in southern and eastern Europe; it is more probable that information on the trends in these parts is so far insufficient.

T a b l e 9. Regional trends in avian range changes in Europe, as revealed by the proportions of different symbols indicating recent changes in the four quarters (N = northern, W = western, S = southern, E = eastern)

| Symbol | N | % | W | % | S | % | E | % |
|--------|------|-------|------|-------|------|------|------|-------|
| + | 332 | 20.3 | 223 | 16.2 | 92 | 6.8 | 176 | 10.8 |
| 0 | 842 | 51.4 | 758 | 55.2 | 825 | 60.9 | 991 | 60.9 |
| - | 327 | 20.0 | 317 | 23.1 | 167 | 12.3 | 327 | 20.1 |
| ? | 136 | 8.3 | 76 | 5.5 | 270 | 19.9 | 131 | 8.1 |
| Total | 1637 | 100.0 | 1374 | 100.0 | 1355 | 99.9 | 1624 | 100.0 |
| Ratio +/- | | 1.02 | | 0.70 | | 0.55 | | 0.54 |

CONCLUSIONS

As we have seen, the bird fauna of Europe has experienced striking changes in recent time. Decreases have been more frequent than increases, which indicates a gradual impoverishment of the fauna. An analysis of the reasons for these changes falls outside the scope of this paper. But it seems quite clear that the main part of all the decreases and increases have been caused directly or indirectly by man. Large number of species have suffered from loss of habitats, due to destruction of old forests, drainage of wetlands, regulation of rivers and lakes, cessation of grazing on shore meadows, introduct-

ion of new methods in agriculture and forestry, different kinds of modern land use, and so on. Pollution by pesticides, human disturbance, hunting and direct persecution have been additional negative factors. On the other hand, remodelling of the environment by man has created new, favourable habitats, or improved the former ones, for a number of species, often with rapid growth and expansion of the population as a result. Several species also have benefited from more efficient protection.

Our responsibility for the future of birds in Europe lays us under certain obligations. In every country, the population changes should be monitored by as reliable methods as possible, so that detailed information can be obtained from all parts of Europe. For the decreasing species, effective measures should be taken to protect them and to improve their living conditions. After a few years, the next analysis of the changing status of European birds will show how well we have been able to fulfil our obligations.

SUMMARY

The changing status of 377 European breeding birds was analysed on the basis of reports from 30 countries. For each species, four alternative symbols were used indicating its status in a given country: increase, no change, decrease or status unknown. On the basis of the distribution of the symbols, the species were divided into seven categories: (1) largely no change: 134 species or 35.5%; (2) no change or decreasing: 91 species or 24.1%; (3) no change or increasing: 48 species or 12.7%; (4) decreasing in some parts, increasing in others: 44 species or 11.7%; (5) largely decreasing: 29 species or 7.7%; (6) largely increasing: 25 species or 6.6%; (7) status largely unknown: 6 species or 1.6%. For each category, the species are listed and some examples presented in maps. Although certain sources of error are involved in the method used, the general trends which emerge from the results are considered reliable. In most orders, decreases exceed increases, this being most striking in Coraciiformes, Galliformes, Gruiformes, Falconiformes, Charadriiformes and Strigiformes. Only in N Europe does the number of increasing species equal that of decreasing birds; in other parts of Europe decreases clearly predominate. The main part of the changes are assumed to be caused directly or indirectly by man.

ACKNOWLEDGEMENTS

# RECENT CHANGES IN THE RANGES OF NORTH AMERICAN BIRDS

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In contrast to conditions in Europe, almost the entire North American continent has undergone massive changes in habitat during the past three centuries. Nearly all of the virgin forest has been cut and nearly all of the virgin prairie sod has been broken by the plow. A high percentage of the original marshlands (including the coastal marshes) has been drained or filled, and thousand of kilometers of rivers have been dammed to form reservoirs and ponds. As the human population expanded and the eastern villages grew and merged with each other, many of the small farms disappeared. In the Midwest as the farming operations became more mechanized the farms became larger and monocultural, and as the demand for grain increased, more of the drier plains were put into cultivation. Although bird populations were poorly documented prior to the middle of the 20th Century, it is certain that the birds were quick to respond to the extensive changes in habitat. The changes that we are witnessing today are only a continuation of those of past decades.

There is no good documentation of population changes of nongame birds in North America prior to 1966 when the Breeding Bird Survey was initiated.This annual survey, which is sponsored jointle by the U.S. Fish and Wildlife Service and the Canadian Wildlife Service, consists of about 2400 randomly distributed roadside routes of 50 stops each (0.8 km apart) at which birds are counted for 3 minutes (Robbins, Van Velzen, 1969). There is a coordinator in each state and each Canadian province who helps select qualified volunteers to run each of the routes. Instructions, maps, and printed forms are supplied by the U.S. Fish and Wildlife Service and the Canadian Wildlife Service, and the results are entered directly onto magnetic tape from the reports received from the observers. After going through a series of edit checks, the data are analyzed by computer to measure year-to-year changes in the population of each species and to calculate long-term population trends. Various reports are generated for the observers, the coordinators, and for research purposes; and computer-generated maps are prepared for selected species. The illustrations that follow are based primarily on Breeding Bird Survey data for the years 1966 through 1979.Because of a change in computer equipment, there has been a delay in processing the data for subsequent years.

Most of the recent changes in range of North American birds fall into one of seven categories. The first I shall discuss is introductions by man. Distributional changes tend to be most rapid in situations where man has introduced a species into a favorable environment. There are a few species whose range is expanding so rapidly that one can connect the outlying localities by a series of concentric lines representing expansion over short intervals of years. The expansion of the eastern population of the House Finch (Carpodacus mexicanus) at 4-year intervals, based on the Breeding Bird Survey, is shown in Figure 1. This western species was illegally liberated in the East by cage-bird dealers.
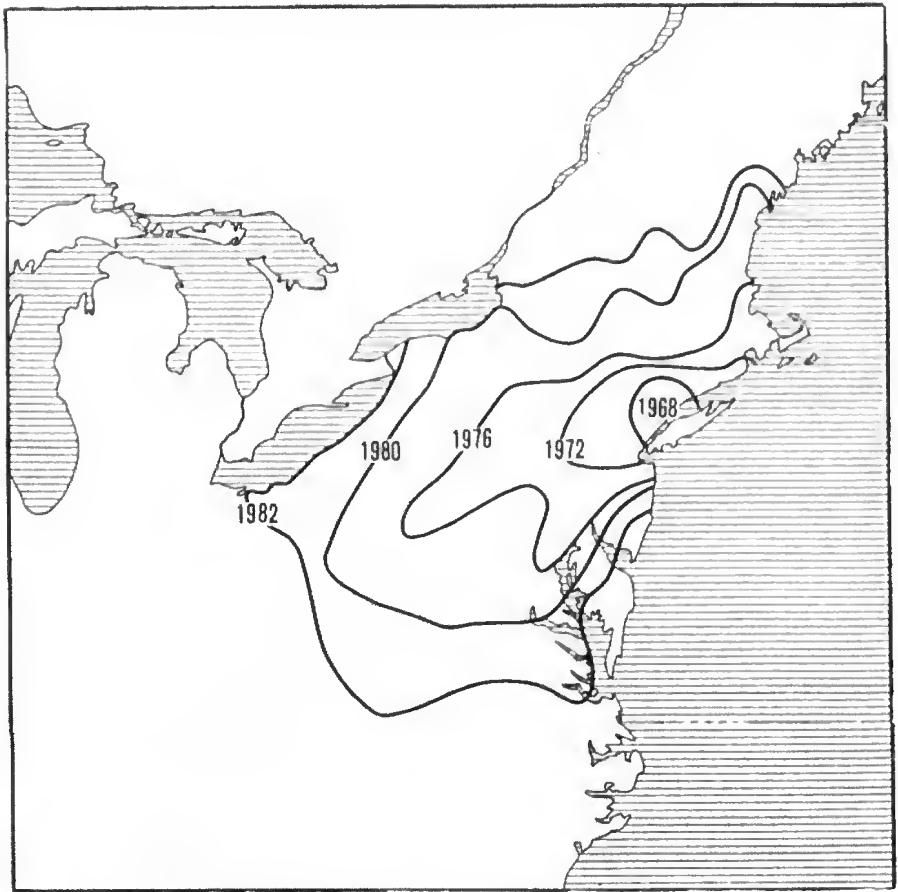
F i g. 1. Range expansion of Carpodacus mexicanus

Another example of an introduced species is the European Starling (Sturnus vulgaris). The limits of its distribution in 1966 were similar to those of today except that it has extended its breeding range a few kilometers closer to the Mexican border. However, the limits of the distribution show only a small part of the story. More important is the spread to additional localities within the range already occupied. Rather than show only the extension of the outer limits of the breeding range, I have outlined in Table 1 those states and provinces in which an important increase took place in the percentage of routes that reported this species. The last two columns show the percentage of Breeding Bird Survey routes that reported each species in the specified geographic area in 1968 and in 1979. A similar technique will be followed for most of the other species discussed.

The Mallard (Anas platyrhynchos) is a native species that nests in almost every state and Canadian province. During the short period covered by theBreeding Bird Survey, however, the breeding population has greatly increased over a substantial part of its range. The reasons for this include the large increase in number of farm ponds and the release of large numbers of hand-reared birds for hunting purposes. In three separate areas of the continent (Table 1) the proportion of routes reporting Mallards more than

Table 1. Changes in the percentage of Breeding Bird Survey routes on which selected species were recorded, 1968 to 1979

| Species | Area | Percent of routes | |
|---|---|---|---|
| | | 1968 | 1979 |
| Bubulcus ibis | Texas and Oklahoma east and north to Pennsylvania and New Jersey | 12% | 29% |
| Anas platyrhynchos | Washington, Oregon, and Idaho | 18% | 43% |
| | 18 states: Colorado and New Mexico east to the Carolinas and Delaware | 6% | 20% |
| | Massachusetts, Vermont, New Hampshire, and Maine | 3% | 8% |
| Zenaida macroura | Massachusetts, Vermont, New Hampshire, Maine, and the Maritime Provinces | 41% | 62% |
| Petrochelidon pyrrhonota | 10 states: Kentucky and Alabama east to Maryland and Florida | 2% | 6% |
| Hirundo rustica | Arkansas, Tennessee, and North Carolina | 76% | 90% |
| | Texas east to South Carolina and Florida | 23% | 61% |
| Parus bicolor | Pennsylvania | 66% | 77% |
| | New York and New England (except Maine) | 10% | 28% |
| Thryomanes bewickii | Illinois and Mississippi east to Pennsylvania and Virginia | 11% | 3% |
| Mimus polyglottos | Ontario, New York, and New England | 8% | 23% |
| Lanius ludovicianus | Iowa and South Carolina north to Ontario, New York, and Quebec | 8% | 2% |
| Sturnus vulgaris | Montana, Colorado, and Lousiana to the West Coast | 52% | 69% |
| Cardinalis cardinalis | Massachusetts, Vermont, and New Hampshire | 10% | 47% |
| Quiscalus mexicanus | New Mexico to Kansas and Oklahoma | 5% | 25% |
| Quiscalus quiscula | Alberta, Saskatchewan, and Montana | 19% | 46% |
| Molothrus ater | North Carolina to Florida | 38% | 65% |

doubled between 1968 and 1979. Even though there was essentially no change in the outer limits of breeding distribution, the doubling of frequency of occurrence over such a large portion of the total breeding range is of major importance.

While discussing man-assisted range expansions, mention should also be made that many species of exotic parrots (Psittacidae) have been liberated in the southern states, especially southern Florida, southern Texas, and southern California. The Monk Parakeet (Myiopsitta monachus) became established at dozens of localities, some as far north as New York and New England; a concerted effort was made to retrieve these birds, however, and now very few of them still persist in the wild.

A second major category of range expansions can be attributed to specific

conservation efforts. This can best be illustrated by the herons and ibises (Ardeidae and Threskiornithidae). Several of these species were nearly exterminated by plume hunters during the first quarter of the 20th Century. Action by conservation organizations and government agencies has resulted in giving protection to the birds and many of their major nesting colonies. As a result, populations have expanded dramatically, especially along the Atlantic coast. The northern breeding limit of the Snowy Egret (*Egretta thula*), for example, was southern North Carolina in 1931, southern New Jersey in 1957, and southern Maine in 1982. The Cattle Egret (*Bubulcus ibis*), which invaded Florida from South America, is still spreading rapidly to the north and west.

A third category of range expansions includes those permanent resident species that have benefited from artificial feeding. I shall give three examples. The Tufted Titmouse (*Parus bicolor*) reached a high population in the Chesapeake Bay area in 1966 and this was reflected by an expansion into the Northeast (Robbins, Van Velzen, 1974). The percentage of routes recording this species in Pennsylvania and in states to the north are shown in Table 1. Thanks to abundant supplies of food at thousands of residential feeding stations, this species has been able to survive the severe winter weather of the northeastern states. The Mockingbird (*Mimus polyglottos*) first appeared in the Washington, D.C. area late in the 19th Century, but its progress farther to the north has been slow until the last 2 decades. Thanks partly to the widespread planting of *Rosa multiflora* hedges and to winter feeding, this nonmigratory species is now surviving much farther north than ever before (Table 1). The Northern Cardinal (*Cardinalis cardinalis*) was hardly more than a straggler in central New England until the 1950's, but it has shown a strong increase during the short period covered by the Breeding Bird Survey (Table 1).

A fourth category includes the westward expansion of woodland birds onto the Great Plains as a result of the planting of shelterbelts. A shelterbelt is a multi-row strip of trees and shrubs that are adapted to the dry, windy conditions of the plains. These plantations have provided nesting sites for many tree-nesting species that were previously restricted to riparian woodlands in those portions of the United States and Canada. The Common Grackle (*Quiscalus quiscula*) has been spreading rapidly into Alberta, Saskatchewan, and Montana (Table 1). The Blue Jay (*Cyanocitta cristata*), which nests primarily east of the Great Plains, has now been recorded at least sporadically in British Columbia and all of the western states.

A fifth category contains those species that are taking advantage of large human structures, such as super-highway bridges and dams. One example is the Barn Swallow (*Hirundo rustica*), a common breeding species throughout most of the United States, but one that until recently has been rare and local in the southeast. See Table 1 for the slight increase in Arkansas, Tennessee, and North Carolina at 35° n. lat., and the much greater increase in the states to the south. The Cliff Swallow, also known as the Eave Swallow (*Petrochelidon pyrrhonota*), nests traditionally on cliffs, and also under the eaves of unpainted barns. During the first half of the 20th Century there was a sharp decrease in populations of this colonial-nesting species as the number of unpainted barns decreased. The birds were unable to attach  their mud

nests to well-painted surfaces. Thanks to the availability of dams and of large bridges constructed in connection with the interstate highway system, there has been a new resource available for attachment of mud nest. *Petrochelidon pyrrhonota* has not only reoccupied its former range, but has spread rapidly southward, and one colony has already been reported from the state of Florida (Table 1).

A sixth category includes those species whose winter survival has been assisted by the recent trend to large-scale mechanical harvesting of grain. The Mourning Dove (*Zenaida macroura*) is a common nesting bird throughout the continental United States and southern Canada. It is one of the most important game species in the central and southern states. The greatest recent range expansion has been in central and northern New England and the Maritime Provinces (Table 1). Mechanical harvesting of grain has benefited all of the granivorous species of Icteridae and is largely responsible for the big increase in *Quiscalus quiscula* to which reference has already been made. Another species in this same genus, the Great-tailed Grackle (*Quiscalus mexicanus*), formerly nested only as far north as Texas. From 1968 to 1979 there was a five-fold increase in the percentage of routes recording this species in the states of New Mexico, Oklahoma, Kansas, and the northern panhandle of Texas (Table 1). The increase of a brood parasite, the Brownheaded Cowbird (*Molotrus ater*), into the southeastern states (Table 1) has been a subject of concern because of the effect this will have on other species that have not previously been exposed to cowbird parasitism.

Up to now we have discussed only range expansions. The seventh category includes the many woodland and open-country species that are gradually retreating as advancing urban sprawl replaces their required habitat. Most strikingly affected are those species in the families Parulidae, Vireonidae, Thraupidae, Turdidae, and Tyrannidae that require large tracts of undisturbed forest during the breeding season. As woodlands become more and more fragmented and isolated by suburban development, reservoirs, highways, transmission lines, airports, and other major disturbances, these neotropical migrants gradually disappear. Recent studies (Robbins, 1979, 198; Witcomb et al., 1981) have shown that the smaller an isolated woodlot is, the few species of neotropical migrants will be found nesting in it.

Finally, there are two declining species of passerines that deserve special mention. One is the Loggerhead Shrike (*Lanius ludovicianus*), which used to nest in every state and most Canadian provinces. It is still common in the southern states, but is disappearing from the northeast (Table 1). Suburban expansion, more intensive farming, removal of hedgerows, insect control, and the severe winters of 1976-1977 and 1977-78 have probably all contributed to this decrease.

The decline of the Bewick's Wren (*Thryomanes bewickii*) east of the Mississippi River is not so easy to explain. This drop was approximately as severe as that for the Loggerhead Shrike in the northeast. *Thryomanes bewickii* has almost completely disappeared from the eastern portion of its breeding range in the Appalachian Mountains, and the few remaining populations in other areas east of the Mississippi River are rapidly dwindling. Although competition with the House Wren (*Troglodytes aedon*) has been sug-

gested as one reason for the decrease, the House Wren does not nest in the southern portion of the range of the Bewick's Wren.

In conclusion, I wish to point out that the percentages in Table 1 relate to the percentage of 50-stop Breeding Bird Survey routes on which the species was recorded and measure changes in the distribution of a species rather than changes in its numerical abundance. Indices of abundance also are available from the Breeding Bird Survey, but for purposes of this symposium it was felt that changes in distribution rather than changes in relative abundance were needed.

SUMMARY

The North American Breeding Bird Survey has provided an annual index of population change since 1966. About 2400 randomly distributed roadside routes of 50 three-minute stops each provide the basic data for computer analysis. One of the reports produced shows the percentage of routes on which each species is encountered in each state and each Canadian province. This percentage is used to show expansion and contraction of breeding ranges and also important changes in frequency of encounter within various portions of the range of each species.

Most of the recent changes in range fall in one of these 7 categories: (1) introduced species; (2) species given special protection; (3) species benefiting from artificial feeding in winter; (4) species taking advantage of shelterbelts; (5) species nesting on large highway bridges and dams; (6) species that feed on grain lost during mechanical harvesting; and (7) species losing habitat as a result of urban expansion. Examples of each category are supported by changes in the rate of encounter.

R e f e r e n c e s

American Ornithologists' Union. The A.O.U. Check-list of North American Birds. 5th ed. Washington, D.C., 1957. 691 p.

Robbins C.S. - In: Workshop Proceedings: Management of North Central and Northeastern Forests for Nongame Birs / Eds. R.M.DeGraaf, K.E.Evans. U.S. Forest Serv. Gen. Tech. Rept. NC-51, 1979, p. 198-212.

Robbins C.S. - Atlantic Naturalist, 1980, 33, p. 31-36.

Robbins C.S., Van Velzen W.T. The Breeding Bird Survey, 1967 and 1968. U.S. Dept. of the Interior, Fish and Wildlife Service, Special Scientific Report-Wildlife 124, 1969. 107 p.

Robbins C.S., Van Velzen W.T. - Acta Ornithologica, 1974, 14 (8), p. 170-191.

Whitcomb R.F., Robbins C.S., Lynch J.F. et al. - In: Forest Island Dynamics in Man-Dominated Landscapes. Ecological Studies 41 / Eds. R.L.Burgess, D.M.Sharpe. N.Y.: Springer-Verlag, 1981, p. 125-205.

# RECENT EXPANSION OF THE SCARLET ROSEFINCH (CARPODACUS ERYTHRINUS) IN EUROPE

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## INTRODUCTION

The avian fauna of a certain area is seldom stable. This has clearly been shown with respect to northern Europe during the last 150 years by, for instance, Kalela (1949, 1955), Niethammer (1951), Mošansky (1964), Väisänen (1969), von Haartman (1973, 1978), Nowak (1975), and Järvinen, Ulfstrand (1980). During the period 1850-1970 Denmark, Norway, Sweden and Finland were colonized by an average of 2.8 species and lost 0.6 species per decade and country (Järvinen, Ulfstrand, 1980).

The recent spatio-temporal expansion of the Scarlet Rosefinch (hereafter called Rosefinch) in Europe is well documented (cf. Bozhko, 1980 and refsrences therein) as is also its breeding biology (e.g. Reinikainen, 1939; Risberg, 1970; Peiponen, 1974; Bozhko, 1974, 1980; Stjernberg, 1979; Zimin, 1981). Stjernberg (1979) has also studied its population dynamics. Hence a caused analysis of the Rosenfinch's expansion could reveal features of general relevance.

This paper summarizes the expansion of the Rosefinch in Europe since the 1930s and discusses the probable processes and factors causing this range extension.

## RANGE EXPANSION AND INCREASE IN NUMBERS

From the extensive and thoroughly compiled data (up to 1976) of Bozhko (1980) on the Rosefinch's expansion in Europe, and countrywide compilations by others (for references, see Bozhko, 1980; von Haartman 1973; Stjernberg, 1979; recent European avifaunistic literature has also been consulted), the following features emerge concerning the expansion during this century:

1. In the 1930s and especially in the 1940s the Rosefinch expanded rapidly to the west and northwest of Finland. Although the first individuals reached the central parts of the west coast in the 1940s, it was not until the 1950s and the 1960s that a rapid increase in numbers was recorded there. In the 1960s the Rosefinch expanded to southwestern Finland and to the Åland islands, and to approximately 66° N lat. in northern Finland. (Helo, 1972; von Haartman et al., 1972; von Haartman, 1973; Rauhala, 1980). Now the species breeds regularly up to c. 66°30' N lat. (Fig. 1).

In parallel with the widening of the Rosefinch's breeding range, both the numbers and densities ross in Finland. The increase in numbers from the middle of the 1940s to the middle of the 1970s was about 30-fold (Järvinen, Väisänen, 1976, cf. also Figs. 2-4; the low densities in the coast parts of Ostrobothnia in Fig. 4 are not real, see Fig. 2).

2. When the rapid increase in numbers and subsequent rangs expansion in Finland in the 1950s and 1960s was well under way, the expansion front advancsd to Sweden (Fig. 5). Since 1954 the Rosefinch has bred annually in Sweden (Risberg, 1970). In the 1950s most of the birds were found in Co. Da-
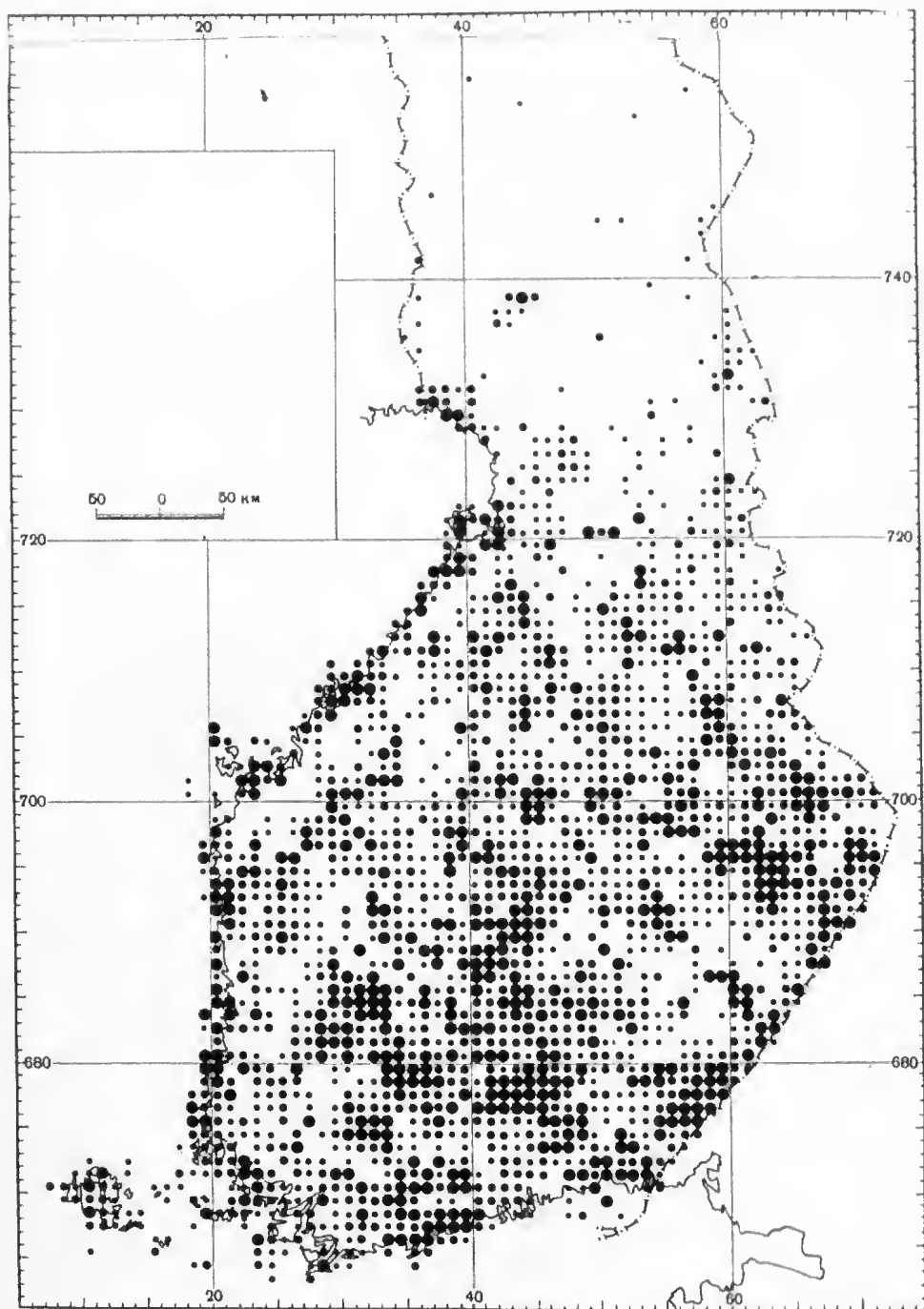
F i g. 1. The distribution of Carpodacus erythrinus in Finland according to
Bird Atlas data 1974-1978, plotted on a 10x10 km grid. Large dot – estab-
lished breeding (Atlas indices 13-20), medium dot – probable breeding (in-
dices 5-12), and small dot – possible breeding (indices 2-4) (Kalevi Hyytiä,
pers. comm.). The lateral figures refer to the Uniform Grid system, Grid27°E
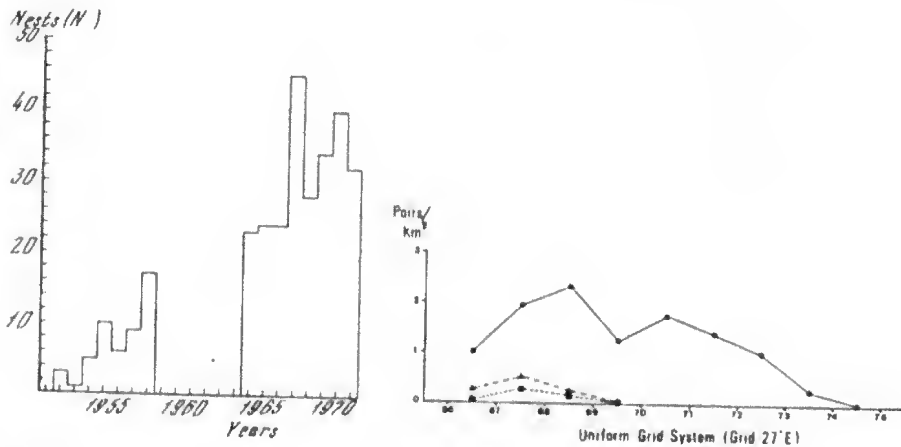
F i g. 2. The immigration of Carpodacus erythrinus into a study area in Kristinestad, western Finland, in 1952-1972. During the periods 1948-1958 and 1965-1972, an active search was made for nests (from Stjernberg, 1979)

F i g. 3. Population trends of Carpodacus erythrinus in Finland during three periods according to line transect censuses. Square = density 1936-1949, triangle = 1952-1963, and dot = 1973-1977. Horizontal axis = northern latitudes, Uniform grid system, Grid 27°E (redrawn from Järvinen, Väisänen, 1982)

larna and Co. Gotland, but in the early 1960s Co. Gästrikland and Co. Öland were also occupied (Rodebrand,1975; Risberg, Risberg, 1975; Fig. 6). In the late 1960s and during the 1970s the Rosefinch spread over large areas in Sweden and the numbers increased manyfold (No. of recorded males: 31 in 1958, 101 in 1964, 371 in 1969 and 1409 in 1974 (Risberg, Risberg, 1975). The numbers of males recorded in Umeå, northern Sweden, rose from 6 in 1969 to 56 in 1974 (Risberg, Risberg, 1975).

3. In the 1970s when the increase in Sweden was rapid, the first pioneers reached Norway. Here the first Rosefinch nest was found in 1970 (Gundersen, 1970), only 12 sightings during the breeding season were known earlier, all from the 1960s (Haftorn, 1971; Larsen et al., 1979). Most of the Norwegian pairs now breed in the southeastern and southern counties, especially in Co. Oppland and Co. Buskerud, but nests have also been found in Co. West-Agder (Bergersen, 1975; Olsen, 1975). In the 1970s Rosefinches have also been recorded during the breeding season along the west coast up to Co. More, Romsdal and Co.Sor-Trondelag (Sandvik, 1980; Follestad, 1981).

During the late 1970s, the increase in Rosefinch numbers in Norway was rapid. From the bird observatory Jomfruland on the outer skerries in southern Norway, the following figures were reported: during 1972-1977 1-6 birds annually, in 1978 10 and in 1979 115 (Cleve, Lifjeld, 1980). Compilation of the

F i g. 4. Densities (pairs/km$^2$) of <u>Carpodacus erythrinus</u> in Finland according to line transect censuses in 1973-1977. The lateral figures refer to the Uniform grid system, Grid 27°E (from Järvinen, Väisänen, 1982)

breeding season observations in the Norwegian avifaunistic literature gives the following minimum numbers: in 1970-1973 annually 3-5 males, 1974-1978 17-35 and 1979 c. 200 males.

4. The first breeding season observation of a Rosefinch in Denmark is from 1966 (Rabøl, 1966); from 1968 onwards it has been observed regularly during the breeding season and in 1972 the first nest was found on Christiansø near Bornholm (Sörensen, 1974). The second nest was found in 1976 on Falster (Franzman, 1977). Most observations are from the eastern islands, especially from Bornholm and Christiansø. The numbers of Rosefinches observed in Denmark have risen during the 1970s, concurrently with the rise in numbers in the neighbouring countries (GDR, FRG, Sweden, Norway).

5. An increase in Rosefinch numbers has also occurred in the northwestern parts of the USSR since the 1930s and 1940s; in the Carelian SSR the numbers

F i g. 5. The range of more or less regular occurrence of Carpodacus erythrinus in Fennoscandia since 1955. Data from Nordström (1956), von Haartman (1973), Risberg (1970), Risberg, Risberg (1975), Stjernberg (1979) and Järvinen, Väisänen (1982). Avifaunistic notes made in Norway and Denmark up to 1981 are also considered; cf. also Fig. 1

have grown rapidly and high densities have been recorded during the 1960s and 1970s (Fig. 4). Now the bird's range extends up to the coast of the White Sea (Bozhko, 1980).

6. In Central Europe the Rosefinch has extended its breeding range in two directions: westward expansion along the Baltic coast began in the 1930s and was still continuing in the 1970s (Lambert, 1979); a southwestward advance became evident in the 1950s and was especially pronounounced during the 1960s and 1970s, mainly along rivers and mountain valley (see Bozhko, 1980 and references therein). The spreading along the Baltic coast has been slow and gradual (Müller, 1973; Lambert, 1979; Bozhko, 1980), but the expansion inland has been more rapid and sudden. The Rosefinch has become a regular breeding bird in Poland (Tomialojc, 1976), and has bred in Czechoslovakia since the 1960s (Darola, Štollmann, 1977) and in Austria since the 1970s (Czikeli, 1976). In Yugoslavia the first Rosefinch nest was found in 1978 (Šere, 1980). In the 1970s Rosefinches have also been observed during the breeding season in the southern FRG (Czikeli, 1976; Lévêque, 1981). Mark Brandenburg/GDR
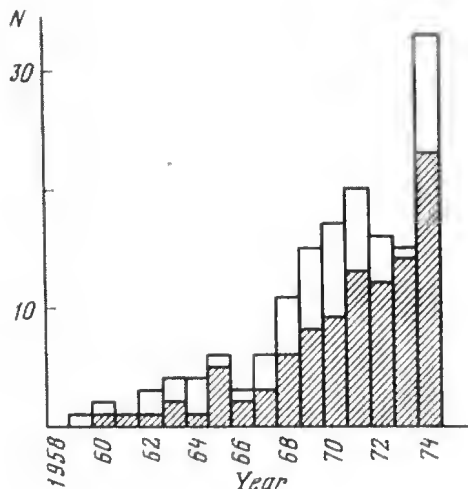
F i g. 6. Annual numbers of loca-
lities and new localities (white
columns) where Carpodacus erythri-
nus was found in the Co. Öland,
E Sweden, in 1958-1974 (from Ro-
debrand, 1975)

(Dittberner et al., 1979), Switzerland (in 1979, 1980, 1981; Lévêque, 1981,
and in litt., Fuchs, 1980; Juon, Bürkli, 1981), France (1977; J.Sharrock,
in litt.), and Bulgaria (1979; Anon, 1982). The number of Rosefinches obser-
ved in spring in Britain and Ireland has risen considerably during the late
1970s (Sharrock, Sharrock, 1976; J.Sharrock, in litt.), and in 1982 the first
nest was found in Scotland (I. Newton pers. comm.).

7. A characteristic feature of the colonization of Fennoscandia, and of the
inner parts of Central Europe as well, is that one-year-old males (grey plu-
mage) have suddenly appeared as far as hundreds of kilometres outside the
normal range of the species, or in previously unoccupied localities within it.
At times local populations have been established forming centres of secondary
spreading.


CAUSES OF EXPANSION

The expansion of the Rosefinch is largely a question of population growth;
more fledglings are being produced than are needed to keep the population in
equilibrium. Hence factors affecting both population dynamics and dispersal
are involved (cf. also Kalela, 1955; Nowak, 1975). The following discussion
will mainly concern Finland but is presumably valid for the whole European
range of the species.

The strong expansion in Finland observed since the 1940s must have been
preceded by some earlier changes in productivity (for definition, see Stjern-
berg, 1979:70). In the 1930s the temperatures in May and June were higher
than during earlier decades (Siivonen, Kalela, 1937; von Haartman, 1973) and
the vegetation was most probably more developed at the start of the breeding
of the late arriving (second half of May) Rosefinch. The nesting success has
been shown to fluctuate strongly from year to year (Stjernberg, 1979) and the
main factor responsible is presumably the extent to which the vegetation has
devellped at the beginning of the breeding season, and the consequent degree

of concealment of its rather conspicuous nest. Nests in closed biotopes are especially exposed to predation. The favourable summers of the 1930s therefore most likely initiated a rise in the nesting success of the Rosefinch.

During this century drastic changes have been caused directly and indirectly by man in the landscape of Finland, Sweden and the USSR (for details, see inter al. von Haartman, 1973, 1978; Ahlén, 1977; Järvinen et al., 1977; Stjernberg 1979; Bozhko, 1980; Hildén, Hyytiä, 1981). These must be of decisive importance for the still continuing expansion of the Rosefinch (cf. also Józefik, 1960; Risberg, 1970). The changes creating or modifying habitats suitable for Rosefinches can roughly be summarized as follows: clearing of continuous wooded areas, regrowth on abandoned grazing or arable land, coniferous plantations, and spreading of human settlement. These changes have occurred both within and outside the normal range of the Rosefinch.

During the last few decades in Finland the Rosefinch's biotope preference seems to have changed towards more open biotopes, approximately in parallel with the increase in numbers. In the new open biotope, the production of fledglings is much higher than in the former more closed biotope (Stjernberg, 1979). Thus the change in biotope preference most likely improved the production of potential colonists and facilitated extension of the range. The sharp decline of the Finnish and Swedish Linnet (Carduelis cannabina) population during the 1920s and the 1930s may have facilitated the shift in the Rosefinch's biotope preference; the recent open Rosefinch biotope is almost identical with the classic Linnet biotope. For possible competition between the Linnet and the Rosefinch, see Stjernberg (1979).

If we take into account the changes in temperature, landscape, vegetation and productivity, and also certain species-specific characters of the Rosefinch, we can construct the following, partly hypothetical picture of its expansion (Stjernberg, 1979). The high site-tenacity of breeding Rosefinches combined with growing numbers, caused by an increase in the production of fledglings during the favourable breeding seasons in the 1930s, resulted in a higher population density and greater "population pressure". Earlier, the Rosefinch in Finland mainly bred in cultural groves and in the margins of luxuriant deciduous woods strongly influenced by man (Reinikainen, 1939), i.e. in relatively closed biotopes. It is not unlikely that Rosefinches for which there was "no room" in the such biotopes, still tried to breed in the vicinity of their conspecifics, due to their sociability (cf. also Bozhko, 1980), and that some of them were thus forced to settle in more open biotopes (the species does not breed in closed forests). The difficulty of finding a site in the saturated biotopes would be particularly great for the young birds, which arrive somewhat later than the older ones, and are probably otherwise weaker in competition (Zimin, 1981). The alternatives open to them would be to continue their migration, to refrain from breeding or to settle nearby in another biotope. Young hatched in the new more open biotope might be imprinted on this biotope (Hildén, 1965). Since the Rosefinch is long-lived, and since the breeding success in the new biotope is twice as high as in the closed one (Stjernberg, 1979), the numbers of Rosefinches breeding in open biotopes grew very fast, giving rise to expansion (for the shift in the Rosefinch's biotope preference, see also Bozhko, 1974; Mazzucco, 1974; Czikeli, 1976).

High temperatures during spring migration stimulate birds to disperse more actively than during cold springs (Otterlind, 1954). Besides improving the production of fledglings, the climatically favourable springs in the 1930s may therefore have stimulated the surplus of returning young birds to disperse over larger areas, both within and outside the normal breeding range. Young Rosefinches are less site-tenacious than older birds (Stjernberg, 1979), and, since suitable habitats were available, no obvious berviers existed to hinder an expansion.

Pioneering Rosefinches were observed in western Finland even before the 1930s - why did these birds not succeed in establishing new colonies? Successful colonization of a new area presupposes a sufficient supply of suitable breeding biotopes in which the resistance from the existing community is not too great. Moreover, it is equally important that the sexual partners can find each other, and that chance extinctions of newly established populations are not too frequent. Various circumstances assist the pairs to find each other: high numbers of colonists, concentration of dispersing individuals in certain areas by topographical features or by the distribution of biotopes; whole flocks migrating too far or going astray. The river Dalälven has evidently been important in the colonization of Co. Dalarna, central Sweden (Bylin, 1975), and the rivers and mountain valleys in the colonization of the interior of Central Europe (Mazzucco, 1974; Czikeli, 1976; Darola, Štollmann, 1977; Bozhko, 1980). The Baltic coastline has also had a directing effect on the Rosefinch's expansion (Mazzucco, 1974), and the Finnish west coast presumably served to congregate migrating Rosefinches and thus increase the chances of successful establishment (Nordström, 1956). The uneven distribution of the Rosefinch in the interior of Central Europe is presumably partly the result of a patchy biotope distribution. Finally, it is worth mentioning that adult male Rosefinches seem to migrate more or less singly, while birds with female-like plumage, i.e. females and one-year-old males, migrate in flocks and arrive somewhat later than the adult males. Warm springs following years with a good production of young should result in an unusually high number of colonists.

The fact that the Rosefinch did not succeed in colonizing western Finland before the 1930s could thus be due to the combined effect of several factors: the colonists were too few, suitable biotopes were lacking, and the resistance from the established avifauna was too great. There is hardly reason to believe that expansion was hindered by the climate per se. It is more likely that the rising temperatures in the 1930s initiated growth in numbers within the normal breeding range, whereas expansion was made possible by changing environmental factors both within and outside the range. According to von Haartman (1973), the northward shift of the isotherms is much smaller than the northward movement of the advancing front of several expanding species, which indicates that the amelioration of the North European climate since the 1930s was probably not of major importance for the range extensions. Perhaps the most important feature of the climatically favourable period in the 1930s was that almost all the summers were good for producing fledglings, and hence the number of colonists rose considerably.

## SPECIES-SPECIFIC CHARACTERISTICS FACILITATING EXPANSION

Several characteristics of the Rosefinch facilitate a rapid increase in numbers (Stjernberg, 1979; cf. also Reinikainen, 1939; Risberg, 1970; Bozhko 1974, 1980; Peiponen, 1974; Czikeli, 1976; Zimin, 1981). These include: (1) low adult mortality, (2) strong site-tenacity among birds which have bred once, (3) a wide range of breeding biotopes, (4) a certain breeding sociability, (5) lack of shyness at breeding sites, (6) flock migration in young birds. Furthermore, it has been established that the Rosefinch is a relatively unspecialized forager, having a wide food and foraging spectrum and a wide register of foraging positions. The bill is not strongly specialized and is well suited for consuming buds, seeds and insect larvae. In other words, the species is very versatile in many respects and is well adapted to a dynamic patchy landscape rich in ecotones. Hence the Rosefinch exhibits most of the characteristics of a good colonist (Mayr, 1965).

It must be emphasized that the Rosefinch's habitat selection had differed somewhat between different periods and that local variation has been common. Consequently, the recent "development" in biotope preferences demonstrated in Finland and elsewhere is mainly to be regarded as a process that is still continuing, being partly a reaction to a changing environment and partly the result of improved productivity and an increase in Rosefinch numbers (Kalela, 1955).

No evaluation can yet be made of the importance of the rapid changes of the landscape in the tropical and subtropical regions, and the temperate grasslands where the Scarlet Rosefinch winters. Birds of open land, like the Scarlet Rosefinch, may have profited by these changes (Jarvinen, Ulfstrand, 1980)

The events or factors causing or facilitating the recent expansion of the Rosefinch in Europe are summarized in Fig. 7.
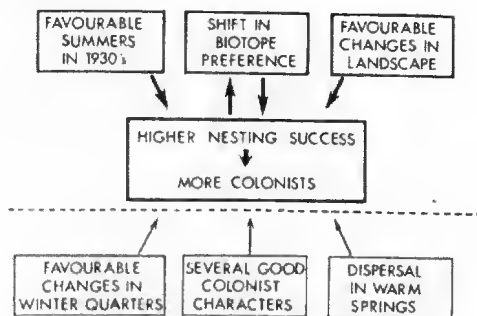
F i g. 7. Events or factors facilitating the recent expansion of Carpodacus erythrinus in Europe, see the text

## SUMMARY

### Recent expansion of the Scarlet Rosefinch Carpodacus erythrinus in Europe

Scarlet Rosefinch numbers have grown manyfold in Europe during the last few decades with a subsequent extension of the breeding range to the north, west and southwest. The countries in which the species now breeds regularly include Sweden (since the 1950s), Norway (since the 1970s), Czechoslovakia (since the late 1950s) and Austria (since the 1970s), and among those from which it has been recorded as a breeding bird are Denmark (1972), Yugoslavia (1978-) and Scotland (1982).

Habitat changes are considered to be the main reason for the recent expansion. The production of fledglings has latterly been much higher than is needed to keep the population in equilibrium. Both factors affecting the productivity and factors connected with the expansion are discussed (Fig. 7).

R e f e r e n c e s

Ahlén I. Faunavård. Om bevarande av hotade djurarter i Sverige, 1977. 256 p. Vällingby.

Anon. - British Birds, 1982, 75, p. 268-272.

Bergersen L. - Sterna, 1975, 14, p. 45-46.

Bozhko S.I. - Acta Ornithol., 1974, 14, p. 39-57.

Bozhko S.I. Der Karmingimpel. Wittenberg Lutherstadt, 1980. 124 p.

Bylin K. Dalarnas fåglar. Dalarnas Ornitologiska Förening. Gävle, 1975. 443 p.

Cleve A., Lifjeld J. - Vår fuglefauna, 1980, 3, p. 160-171.

Czikeli H. - Egretta, 1976, 19, p. 1-10.

Darola J., Stollmann A. - Biológia (Bratislava), 1977, 32, p. 111-120.

Dittberner H., Dittberner W., Sadlik J. - Falke, 1979, 26, p. 296-298.

Follestad A. - Vår Fuglefauna, 1981, 4, p. 177-185.

Franzmann N.-E. - Vögel der Heimat, 1977, 50, p. 262.

Gundersen W.H. - Fauna, 1970, 23, p. 272-276.

Haftorn S. Norges fugler. Oslo; Bergen; Tromsø, 1971. 862 p.

Von Haartman L. - In: Breeding biology of birds. Proc. of a symposium on breeding behavior and reproductive physiology in birds, Denver 1972 / Ed. by D.S.Farner. Wash., D.C., 1973, p. 448-481.

Von Haartman L. - Fennia, 1978, 150, p. 25-32.

Von Haartman L., Hildén O., Linkola P. et al. Pohjolan linnut värikuvin, 1972, XII. p. 985-1092. Helsinki.

Helo P. - Kainuun linnut, 1972, 2, p. 27-75.

Hildén O. - Ann. Zool. Fennici, 1965, 2, p. 53-75.

Hildén O., Hyytiä K. - In: Proc. second. Nordic congr. ornithol. 1979. Stavanger, 1981, p. 19-37.

Jósefik M. - Acta Ornithol., 1960, 5, p. 307-324.

Juon M., Bürkli W. - Orn. Beob., 1981, 78, p. 54-55.

Järvinen O., Ulfstrand S. - Oecologia (Berl.), 1980, 46, p. 186-195.

Järvinen O., Väisänen R.A. - Ornis Fennica, 1976, 53, p. 115-118.

Järvinen O., Väisänen R.A. Ecological zoogeography of Finnish birds. Numbers and long-term changes. Helsinki, 1982.

Järvinen O., Kuusela K., Väisänen R.A. - Silva Fennica, 1977, 11, p. 284-294.

Kalela O. - Bird-Banding, 1949, 20, p.77-103.

Kalela O. - Ann. Zool. Soc. Vanamo, 1955, 16 (11), p. 1-80.

Lambert K. - Ornithol. Rundbrief Mecklenburgs, N.F., 1979, 20, p. 1-8.

Larsen B.M., Opheim J., Østbyee T. - Vår Fuglefauna, 1979, 2, p. 129-135.

Lévêque R. - Orn. Beob., 1981, 78, p. 53-54.

Mayr E. - In: The genetics of colonizing species / Eds. H.G.Baker, G.L.Steb-
    bins. N.Y.; L., 1965, p. 29-47.

Mazzucco K. - Egretta, 1974, 17, p. 53-59.

Mošansky A. - Aquila, 1964, 69-70, p. 173-194.

Müller S. - Corax, 1973, 4, p. 112-130.

Niethammer G. - Bonn Zool. Beitr., 1951, 2, p. 17-54.

Nordström G. - Ornis Fennica, 1956, 33, p. 19-28.

Nowak E. - Zeszyty Naukowe, 1975, 3, p. 1-255. (Translation 1975, Smithsonian
    Institute, Washington, D.C.).

Olsen K. - Sterna, 1975, 14, p. 161-166.

Otterlind G. - Vår Fågelvärld, 1954, 13, p. 1-31, 83-113, 147-167, 245-261.

Peiponen V.A. - Ann. Zool. Fennici, 1974, 11, p. 155-165.

Rabøl J. - Dansk ornithol. Foren. Tidsskr., 1966, 60, p. 77-84.

Rauhala P. Kemin-Tornion seudun linnusto. Kemi, 1980. 172 p.

Reinikainen A. - Ornis Fennica, 1939, 16, p.73-95.

Risberg E. - Vår Fågelvärld, 1970, 29, p.77-89.

Risberg L., Risberg B. - Vår Fågelvärld, 1975, 34, p. 139-151.

Rodebrand S. - Calidris, 1975, 4, p. 3-12.

Sandvik J. - Vår Fuglefauna, 1980, 3, p. 279-282.

Šere D. - Acrocephalus, 1980, 1, p. 13-16.

Sharrock J.T.R., Sharrock E.M. Rare birds in Britain and Ireland. Berkhamsted,
    1976. 336 p.

Siivonen L., Kalela O. - Acta Soc. Fauna Flora Fennica, 1937, 60, p. 606-634.

Stjernberg T. - Acta Zool. Fennica, 1979, 157, p. 1-88.

Sorensen B.M. - Dansk Ornithol. Foren. Tidsskr., 1974, 68, p. 68.

Tomialojć L. Birds of Poland. A list of species and their distribution. Trans-
    lated from Polish by Foreign Sci. Publ. Dept. National Center Sci. Techni-
    cal and Economic Inform., USA.) Warszawa, 1976. 256 p.

Väisänen R.A. - Ann. Acad. Sci. Fennicae, 1969, A IV, 149, p. 1-90.

Zimin V.B. - In: Ecology of vertebrate north-west part USSR, Petrozavodsk,
    1981, p. 13-31.

# THE DECLINE OF THE CORNCRAKE (CREX CREX) IN EUROPE

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The global breeding range of the Corncrake lies largely within the Western Palearctic north of the Alps and Pyrenees to about 62°N. The species is one of the few in the region largely dependent on farmland habitats. Marked population declines have occurred in most regions since the late 19th and early 20th centuries following the introduction of mechanised grass-cutting.

With a bird so difficult to observe, surveys have had to rely on counts of calling birds which are usually, but not inevitably, males. The relationship between numbers of calling birds and pairs is unknown. A high level of vocal activity continues from late May until early July but it is necessary to carry out surveys at night in calm weather.

By the end of the 1970s the population in western Europe was largely restricted to 1200-1500 calling birds in Ireland, chiefly in the northwest (O'Meara, 1979); about 730 in Britain, mostly on islands in northwest Scotland (Cadbury, 1980); 50-600 in Sweden, mostly on two Baltic islands, Öland and Gotland (Rodebrand, 1978; Svenson, 1978); several hundred in Finland (Hilden, pers. comm.); about 100 in the Netherlands, largely in the flood plains of rivers such as the Waal, Rhine and Ijssel (Teixeira, 1979), and perhaps still in some of the river valleys in east and central west France (Yeatman, 1976) and the north-west region of the Federal Republic of Germany (Glutz von Blotzheim et al.,1973).

In eastern Europe detailed information is lacking but marked declines have occurred in much of western USSR (excluding Estonia), the German Democratic Republic, Czechoslovakia, Hungary and Bulgaria (Cramp, Simmons, 1980). The Corncrake is still locally frequent in eastern Poland but has decreased in the west (Tomialojc, 1972 and pers. comm.) and probably eastern USSR.

By the time of the first national survey of the Corncrake in Britain and Ireland, in 1938-39, the species had already disappeared from much of eastern England where farming was most intensive. It was still frequent in northern and western parts of Britain and much of Ireland (Norris, 1945, 1947). The British Trust for Ornithology and Irish Wildbird Conservancy survey of breeding birds of Britain and Ireland, carried out over the years 1968-72, demonstrated a further retreat north-westwards (Sharrock, 1976). In the BTO and IWC surveys of 1978/79, an attempt was made for the first time to count all calling birds, so scarce had Corncrakes become (O'Meara, 1979; Cadbury,1980). Only 10 years after the Atlas survey the number of ten km squares in Britain in which breeding was confirmed or considered probable, declined from 528 to 160, a 70% reduction. The species had all but vanished as a breeding bird from England and Wales and was very scarce in the south-eastern half of Ireland. In Britain, the Corncrake only remained frequent on certain of the Hebridean and Orkney islands in northwest and north Scotland. The number of calling birds was reduced from an estimated 2600 to 730. Of the ten km squares in which Corncrakes were probably breeding, only 6% supported more than

15 calling birds. The highest densities, which ranged between 6 and 11 per km$^2$, were all on small-holdings (crofts) with small fields, non-intensive farming and much marginal habitat.

Breeding populations of this migratory bird appear to be subject to fairly marked annual fluctuations. On the island of Tiree, off the west coast of Scotland, early July counts of calling Corncrakes in six years between 1969 and 1979, ranged between 50 and 98 with a mean of $74.0 \pm 18.8$ (Cadbury, 1980). The monitoring of the Irish population has indicated a continuing decline since 1978.

The habitat from which Corncrakes were calling was recorded for 530 birds in Britain in 1978-79. 61% were in grass cut for hay or silage. However, in the Outer Hebrides, a Corncrake stronghold, about half the 183 birds in May and June were in marshy areas where stands of tall Iris pseudacorus and Phragmites australis were favoured. In one area the habitat of calling birds was recorded again in July, after the hay was mown. Twelve of the 16 birds which remained relatively sedentary were in marshes. Of the 15 that shifted habitat, 9 moved to weedy oat Avena fatua/strigosa crops (Cadbury, 1980). 20% of the calling Corncrakes recorded in Ireland in 1978 were in marshes (O'Meara, 1979).

Over most of Britain, including Orkney, the grass in the majority of meadows cut for silage or hay, has been sown (leys) or improved with fertilizers. In the Outer Hebrides and on Tiree, where crofting still prevails, only a third of the meadows in the late 1970s were leys or otherwise improved. Natural meadows had a greater variety of plants (an average of 11 or 12 species) than improved grass (9 or 10 species) and leys (6 species). On the other hand, in both areas, the height of the sward of "natural" meadows was only two thirds that of leys ($P < 0.01$) when measured in June or early July. The sward in "improved" meadows was intermediate in height. In the Outer Hebrides in June, calling Corncrakes exhibited a preference for leys over "natural" meadows ($P < 0.02$), while on Tiree, in early July, "improved" and "natural" areas were preferred ($P < 0.01$).

Corncrakes have been recorded taking a wide variety of invertebrates as food. In the Hebrides, pitfall traps indicated that carabid and staphylinid beetles were abundant in both natural meadows and leys. Opilionids and large carabids occurred in large numbers in the damp meadows and marshes frequented by Corncrakes in the Outer Hebrides.

Habitat preferences of Corncrakes in the breeding season are likely to be influenced by the need for cover and food. When Corncrakes return to their northerly breeding areas in May there tends to be a lack of suitable vegetation cover. It is not surprising that the birds seek the more luxuriant sown grass and damp fields with clumps of Iris. Leys are, however, unsuitable breeding habitat for Corncrakes because they are cut for silage in June or for hay in the first half of July when birds have nests or small young. Moreover, the dense sward may restrict feeding activities. The improved and natural meadows favoured on Tiree in July are not only mown later than leys but may offer greater food availability for young Corncrakes.

There are several reasons why Corncrakes remain frequent where farming based on small-holdings (crofts) prevails on certain exposed islands off the

west coast of Scotland. The small fields, many less than five ha, offer a
variety of habitats. There are still many "natural" meadows and little silage
is made. Corncrake nests and broods have a fair chance of escaping destruct-
ion. The broad field margins, weedy crops and marshy fields provide alterna-
tive habitat once the hay is cut.

Though the Corncrake avoids swamps favoured by most Rallidae, it clearly
has an association with damp grasslands in many of its remaining strongholds
in western Europe. The species should be included among birds whose wet
meadowland breeding habitat is threatened by drainage. Even in the Outer
Hebrides there are many signs of a lowered water table and shrinking marshes.
A proposed major agricultural improvement scheme in the Outer Hebrides,funded
by EEC and British Government grants, is likely to seriously exacerbate the
situation.

The future for the Corncrake in Europe, even in its present strongholds,
appears bleak. The bird shows no signs of being able to adopt to the envi-
ronment created by more intensive farming. The loss of marshes and other semi-
natural habitat on farmland may be forcing Corncrakes to frequent sown grass
crops were there is little opportunity for successful breeding.

SUMMARY

The long-term decline of the Corncrake _Crex crex_  in western Europe con-
tinues. The species appears to be unable to adapt to the environment created
by intensive agriculture. Though birds are attracted by the cover provided
by grass leys, early mowing for silage has disasterous effects on breeding
success. Damp meadows and marshes, in the flood plains of certain major ri-
vers in the Netherlands, France and the Federal Republic of Germany, in se-
veral areas around the Baltic and on small-holdings in the northwest ex-
tremities of Britain and Ireland, afford the last strongholds of the Corn-
crake in western Europe. Even they are threatened by drainage.

R e f e r e n c e s
Cadbury C.J. - Bird Study, 1980, 27, p. 203-217.
Cramp S., Simmons K.E.L. The Birds of the Western Palearctic. Vol. 2.
    Oxford, 1980.
Glutz Von Blotzheim U.N., Bauer K.M., Bezzel E. Handbuch der Vögel Mittel-
    europas. Vol. 5. Frankfurt am Main, 1973.
Norris C.A. - Brit. Birds, 1945, 38, p. 142-148, 162-168.
Norris C.A. - Brit. Birds, 1947, 40, p. 226-244.
O'Meara M. - Irish Birds, 1979, 1, p. 381-405.
Rodebrand S. - Calidris, 1978, 7, p. 91-96.
Sharrock J.T.R. The Atlas of Breeding Birds in Britain and Ireland. Tring,
    1976.
Sveriges Faglar / Ed. by L.Svensson. Stockholm, 1978.
Teixeira R.M. Atlas van de Nederlandse Broedvogels. Deventer, 1979.
Tomialojc L. Birds of Poland. Warsaw. Translation: Fish and Wildlife Service,
    Wash., 1976.
Yeatman L. Atlas des Oiseaux Nicheurs de France de 1970 à 1975. P., 1976.

# ANALYSIS OF DIFFERENT FACTORS CAUSING DYNAMICS OF BIRDS RANGES

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This is one of the oldest and, at the same time, most lasting questions of both zoogeographers and ecologists: which factors delimit a Species' range? It is just one a combination of diverse factors, is the composition of this complex similar within a taxonomic group or not and, finally, is our knowledge sufficient to predict where an expansion process (or its very opposite) is likely to be stopped by external or internal conditions?

Range expansion of dramatic extent (and this means usually, or dramatic speed) occurs in groups of high mobility and high ecological plasticity - as for instance birds. Therefore, ornithology is largely apt to offer essential clues to phenomenology and theory of chorology.

On the other hand, we neglect here all those cases where most obvious limits (very steep gradients) like the borderline between sea and land, mountains and plain, desert and forest, are responsible.

But, why does the Rock Bunting (Emberizacia) not breed in the Central German Harz mountains or in the eastern Bavarian mountains whereas it does in the ecologically similar Schwarzwald? Why is the Palm Chat (Dulus dominicus) con-fined to Hispaniola while its flying abilities are obviously strong enough to reach Cuba just 80 km farther west? In other species, geographical discontinity does, due to dispersial phenomena, not mean isolation between populations. What urges the Bluetail (Tarsiger cyanurus), the Yellow-breasted Bunting (Emberiza aureola) or, more recently, Cetti's Warbler (Cettia cetti) to protrude into regions where changes of habitats as required by them are not (clearly) visible? Why does one species expand its range, a second one withdraw and a third one keep its home rights as if nothing had happened? Why did the Scarlet Rosefinch (Caprodacus erythrinus) expand its breeding range just in recent years and not half a century earlier? In more general terms: although range (or "area") is clearly not a status but a continued process, why then do most species, mobile as well as plastic, not expand?

These are by far too many questions to be answered within a few minutes. This would mean to press into a ping-pong ball what would fill a medium-sized ballon. Let us see then some of the aspects involved which the author (like some other people) thinks important.

Before doing so, we must confess a serious hindrance which biasses many of our considerations more severely than some of us might be willing to admit: our knowledge of specific ecology is, for the majority of bird species even in Europe, based mainly or entirely on the description of habitat as seen by human eyes, the altitude above sea level and an enumeration of food items. Theorists tend to draw conclusions of - hopefully-high significance, and this is necessary. However, much has been claimed which seemed to be clearly supported by apparently convincing evidence. So it often fell into oblivion that one should look for discordant or falsifying rather than for concordant data, so-called "Instances". A reappraisal is inevitable - and the call for more basic information following other aspects than usually

applied. Yet, much importance has been found out recently and I cannot feel sure not to have overlooked really essential studies.

The factors causing or affecting range dynamics fall onto two major categories. The first one comprise intrinsic factors defined as physiological ecological, and psychological properties that determine way and extent of reaction to barriers of any kind. Genetic conditions and/or changes seem obvious factors of importance, particulary mutations which initiate range dynamics. The evidence, however, is limited. Although pioneer populations might be rather uniformly made up of certain genetic variants, and mutants might form the expansive proportion of them, most phenomena can be explained with more ease. The normal recombination potential should be sufficient to yield preadapted genotypes, and in at least one case a spectacular change-over did not even test the specific valency to say nothing of a fundamental mutative change of behaviour.

Physiological abilities may be fundamental prerequisites or strictly limiting factors (as is temperature resistance or mobility) but not causes of expansion. However, if (for instance) the capacity of nestlings to resist cooling or to respond to heat loads is changed the population will be urged to restrict or to shift its area.

A high reproductive potential (in a dispersive species) raises the probability of dispersal beyond the range limit and is the decisive prerequisite for the quick establishment and stabilization of new local populations. The impressive figures known from North American Cattle Egret (Bubulcus ibis), especially the population increase in Texas illustrate this.

Often a widening or shift of the niche and changes of behaviour have been offered or claimed as important factors. This could be due to either genetic changes or plastic phenomena. Plasticity as understood by the author is "the enlargement of the frame given by the open genetical programme" as "a result of the coupling and switching pattern characteristic of the specific system of niche utilization". It thus depends on the number of system elements that are potentially connectable and of the capacity of coupling them which is determined by the central nervous system. Elements in this sense are, among others, structures and behaviour patterns (like foraging techniques) and preferences for environmental elements specifically utilized. These preferences are directed by specific searching images and largely depend on their number and the degree of their complexity. All this defines the versatility of a species and, hence, its survival chances in other than its herediary habitats. A survey of the characteristics exhibited by successful colonists has been given long ago by Mayr (1965). They are essentially based upon the capacity of plastic reactions.

Sociability is not of decisive significance: single breeders - like the Scarlet Rosefinch (Caprodacus erythrinus) and species dependent on colonies (of other species) as is the Cattle Egret may be successful intruders. Yet, traits of the social and communicative system of a species are often considered helpful in the course of expansion processes as they are in part responsible for the growth of population size which is essential for taking roots in a new area: dispersal in flocks facilitates settling success and the facts having provoked the "information centre hypothesis" lower the mortality rate in colonizing groups.

758

Migratory properties of a species cannot be meaningless here. Udvardy has
summarized as early as 1969: "In addition to single pioneers... wanderings,
migrations, and irruptions may also lead to the establishement of new breed-
ing stations, which can dewelop into new settlements. All are mass phenomena.
Migration movements expose birds to unusual external factors of chorological
significance  (like wind drift and change).Intrinsic causes may become ef-
fective if migratory individuals fail to obey the ortstreue principle. In
one case, defective homing behaviour, they do not return from the winter
quarters to their northern birth or breeding places - everybody knows the
nesting of European White and Black Stores (Ciconia ciconia and C.nigra) in
Africa. In the other case, prolonged migration whatever the causes (cf. hor-
monal processes, degree of philopatry; spring temperatures and development of
vegetation) provides opportunity to settle in places beyond the (average)
range boundary. This has enabled many bird species to settle in regions offering
food supply only part of the year (what simultaneously forces them to exert
periodical migrations, even in the tropics).

Albeit orstreue, site tenacity and homing abilities must be, on one hand
invalidated to enable that widening of range, and it is precisely these capa-
cities which have to be effective, on the other hand, for colonists not to
vanish anywhere after the first migration flight that is enforced by migrat-
ion instinct. An instance is the European Quail(Coturnix coturnix)introduced
into the United States: they dissappeared after summer and never came back.

It should be emphasized here that - notwithstanding the significance of
population status - range size has no bearing on expansiveness.

The most relevant intrinsic factor appears to be dispersability. This
shows clearly in pairs of species which are practically identical in morpho-
logy and mobility but differ sharply in their dispersal patterns. A well-
known example is the Silvereye(Zosterops lateralis)which got over the 2000 km
of open sea between Tasmania and New Zealand and the settled on all outlying
islands whereas a species on the Solomon, Zosterops rendovae, shows no ten-
dency to overcome barriers of just some km width. For most population,however
we may assume non-uniformity as to dispersal ability. Pioneering populations
like those occupying temporary areas of pulsating ranges consist of indivi-
duals which combine dispersal with dismigration or non-philopatry. The two
phenomena might be under separate control but imprinting is, at least often,
likely to play a decisive part as is indicated by removal experiments.

In general: population phenomena and population dynamics as the relation
of productivity, dispersion and mortality form not merely the most important
and most closely connected intrinsic factor but also, the immediate vehicule
of range processes.

Among the extrinsic factors, climate will be named mostly in the first
placs. Basic physical conditions like temperature, rainfall, humidity, ampli-
tude of circadian and circannual fluctuations are considered equally impor-
tant as are secondary phenomena dependent on them (like vegetation and food
supply). Many of the changes of the European, especially the Fennoscandian
avifauna have been discussed as caused or influenced by short-term fluctuati-
ons or long-term climatic changes, the latter even as the final phase of
post-glacial, reoccupation of northern regions.

One basic factor is of most apparent influence: wind as drifting or inhibiting power.Its role should not be overestimated since the Silvereye and the Europian Hedgesparrow (Prunella modularis) have crossed wide expanses of usually turbulent sea around New Zealand and colonized the outlying islands. This shows, however, that difficulties of an active spread cannot be offered as a hindrance in case where far smaller distances have not been bridged.

Every single factor of autecological significance means simultaneously a kind of barrier. Geographical and vegetational barriers are effective in depence on species properties and abilities. Speciation of certain groups, e.g., in Madagaskar is an irrefutable proof that barriers have not been crossed in spite of the mere physical capacity to do so (doubtlessly being given). So, these boundaries are seldom strictly exclusive for dispersable species. Yet, their breakdown or overcoming is not a daily event, and often pure chance decides for or against (see those famous Fieldfares Turdus pilaris having reached Greenland whereas many American parulids did not establish branches in Europe).

Often habitat changes have been alleged to explain boundary shifts. This way apply to many cases although habitat structure have rarely been analyzed to exclude that the differences are not only striking to our eyes but essential for the bird itself. For the same reason, one should be careful before stating a "change in habitat preference".

A newcomer is dependent on structures and resources at his disposal.Two kinds of statements must be criticized in this respect. The first is the socalled "empty niche". As the niche, by defivition, is species-specific it cannot exist without the species or, in Udvardy's working, "until filled". Secondary, the "competitive exclusion principle" or Gauseian hypothesis has been made responsible for species being prevented from invasion into a new habitat by another species that allegedly "occupies the same niche". The ecological system which controls the utilization of environment is a characteristic of biological species as a result of radiative evolution and, therefore, is not likely to be shared by to different species.

To start anew: a new comer must encouter an ecological gap comprising all requirements for his survival. This means, e.g., the absence of a serious competitor (as in the cases of the Cattle Egret in America and the Hedgesparrow in New Zealand), the availability of nesting places (especially for species preferring large mixed colonies), but also the absence of harmful predators and parasites and, in some cases, the presence of attractive ecological partners in trophic relations.

One of the crucial questions,the receptivity of biotopes, has been largely disputed in recent years and will be, from another point of view, indicated later. Compstition mechanisms appear - to the author - to be seen somstimes in too simple a way as to reflect matural connections.

In recent centuries, most obviously in the 20th, one factor has caused or biassed an increasing number of range dynamics processes. It looks like you and me has been named "the Wise man", Homo sapiens. It is hardly necessary to enumerate all influences, direct ones such as active extermination of populations, naturalization of spscies in other regions or strict conservation measures (see the re-expansion of the Raven Corvus corax in Central Europe)

and ondirect influences by changes of environment - between afforestation, deforestation and contamination. Several of the most striking cases of recent expansion have obviously been favoured or even enabled by human activities.

Three basic conditions of active spread are usually regarded: I. dispersion across the boundary, 2. ecological valency or an ecological gap (or a niche holder can be pushed out), and 3. a high reproductive potential. These points are not sufficient for our topic. They show, however, that hardly a single factor can be responsible. A barrier is a barrier only in relation to mobility and dispersability which in turn has to do with territoriality, site tenacity, habitat and food selection, and homing abilities. Such a choose of specific sites reinforces the barrier.

The combined effect of different factors is obvious in three cases to follow. The Black-headed Gull (Larus ridibundus) has, has in many parts of its range, not only increased in numbers but established new colonies within and beyond its boundaries. Besides the increase of breeding sites following eutrophication of many water bodies, it was mainly the decrease of winter mortality caused by rich food supply (feeding of refuse; feeding by humans). So the squilibrium with the reproduction rate was lost and a population increase started. The Hedgesparrow has been introduced to New Zealand. The decisive factors which enabled the impressive spread were the very low level of competition and immense changes of vegetation character (by destruction of many native habitats and acclimatization of hundreds of exotic plant species) which led to new habitat types into which the bird fitted better than any of the specialized endemic species. Moreover, among the acclimatized plants there are many European shrubs and weeds on the seeds of which the bird feeds in Europe."The colonization of remote outlying islands by a small passerine bird without specialized flight abilities may be considered a proof that neither "land-bridge" nor long terms are actually necessary".

The third instance is provided by the enourmous expansion of the Cattle Egret. The population increase in Africa exposed more individuals in their dispersal phase to marine wind conditions. Those arriving in South America encoutered not only suitable habitats and mixed colonies of other areids but also a rich insect fauna and the partners required for the specific feeding strategy: herds of large mammals though not wild species as in Africa but masses of livestock bred by man. So the newcomer lighted upon really optimal conditions.

Range dynamics of some extent have consequences on, firstly, the communities of which the species involved was, or just became a member and, secondly, on the population occupying a new areas. This field, of investigation appears to have attracted less attention than it derives.

The competition system within the committee is affected if a species leaves a gap or if another species has to be incorporated. The changes set going should differ according to the niche character. A species may hold an unique position on all communities as is the case in the Cattle Egret whose foraging strategy keeps competition at a very low rate. Thus, the bird would leave a gap which is not likely to be filled by any other species. The picture is quite different if the species is a member of a guild. Not only has it to cope with these competitors but the latter, conversely, may be urged to apply

more or other belts of their ecological spectra. Strength of competition or
even exclusion depends, moreover, on the size of the guild (the number of
member species). In many cases, this means that ecological péasticity is
tested in either, but it could likewise imply an evolutionary consequence
that will be discussed later.

On the other hand, if a guild member abandones the community it relieves
a specific mosaic of resources from being used. As a model for the conditions
to follow then we can avail ourselves of studies on phenomena of "Ecological
release" on islands where one or more species of a guild lack for chorogical
reasons.

One of the expansion rules more or less generally accepted states that
"optimal" habitats are occupied first of all. The meaning of "optimal" appears
to have been read only as "favourable in structure and climatic conditions"
whereas the most conventient competition pattern in the taxocenosis or, least,
in the guild in diverse habitats might often be the responsible feature.

Another kind of problems arises from the evolutionary point of view. The
changes in the community as just indicated have an improtant bearing also for
the popultion and, hence, for the species itself. The changes in competition
pattern modify the conditions for the genotypes. Ecodogical plasticity may,
for, the first period, be helpful for survival of individuals. Meanwhile, the
gene pool of the population is rather radically reorganized. Certain genotypes
might fit better now than they did in the area inhabited before. Secondly,
other gene combinations may become successful which formed the (more or less
handicapped) "Sleeping" reserve and could not be productive. Furthermore, new
recombination types arise some of which are particulary prosperous. Lastly
new mutation result in new genotypes which likewise have to expose themselves
to selection.

SUMMARY

Range expansion of dramatic extent (and speed) occurs preferentially in
animal groups of high mobility and high ecological plasticity. Analytical
studies of such processes can yield essential clues to phenomenology and
theory of range dynamics no matter which taxonomic group and which type of
change is involved.

As range is a multidimensional space, defined (besides the 3 spatial di-
mensions) also by habitat(s) and time, it is subject to various changes
which – though each case exhibits unique traits – can be grouped into A shift
of (outer) limit, B disjunction of range, C shift of inner limits (including
urbanization), and D changes of density in (marginal) populations.

Factors influencing or causing fluctuations of inner or outer boundaries
are of different character. One group comprises endogenous factors such as
high number of the econtic system (resulting in plasticity dispersal pattern,
population structure and dynamics, reproductive potential, physiological abi-
lities, communication system). Exogenous factors of particular significance:
presence of strict barriers, ecological gap in the potential new area, chan-
ges of environment, presence of ecological partners (useful or harmful). Cau-
sal analyses, however, are often impeded by incompleteness of ecological
data.

# EXPANSION OF AREAS BY 15 BIRD SPECIES
## IN BALKAN PENINSULA

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During 45 years the author together with his collaborators was making ob-
servations and analysing the process of expansion of areas by 15 bird species
in Yugoslavia. Bulgarian and Rumanian ornithologists were also interested in
this subject.

The expansion of areas was being observed in the central, northern and
western parts of Balkan Peninsula and also in the foothills of East Alps by
the following bird species: Phylloscopus trochilus, Streptopelia decaocto,
Dendrocopus syriacus, Hirundo daurica, Hirundo rupestris, Corvus frugilegus,
Hippolais pallida, Oenanthe hispanica, Ficedula hypoleuca, Ficedula semitor-
quata, Turdus pilaris, Passer hispaniolensis, Passer italiae, Carpodacus
erythrinus, Cisticolla juncidis.

While the preparatory work for field investigations and summarysing of
the results the insufficient study of outlying parts of the area and the
dynamics of the very process of settling were taken into account.

At the Fig. 1-8 you can see the dynamics of this process. Thus the data
concerning areas is generalized and schematized.

It was usually considered that only southern bird species expand the areas
of their distribution to N and NW. In Balkan Peninsula it was observed for:
Streptopelia decaocto, Dendrocopus syriacus, Hirundo daurica, Hirundo ru-
pestris, Hippolais pallida, Oenanthe hispanica.

But at present we can also see the reverse process in Balkan Peninsula -
the extension of arees to S: Phylloscopus trochilus, Ficedula hypoleuca,
Turdus pilaris, Carpodacus erythrinus, and Corvus frugilegus expands the
area of its distribution to S and W.

According to the information of Bulgarian ornithologists Ficedula semi-
torquata is also expanding the area of its distribution to W.

Distribution of two bird species: Cisticolla juncidis and Passer italiae
from W to E was for the first time observed on the territory of Yugoslavia-
according to the data based on the investigation of hybrid population si-
tuated at the junction of areas with Passer domesticus, Passer italiae is an
independent species.

Two groups of reasons are known to make birds expand their areas on Bal-
kan Peninsula:

1. Changes in the ecological position in which a man introduces most im-
portant alterations.

2. Changes in the very bird organism.

In most cases both reasons are closely interconnected and complicated
with climate fluctuations. Take, for instance, Mediterranean migrating
birds, their nesting outside the nesting area far to N was being observed
during the years with especially warm and arid springs.

F i g. 2. Distribution of Passer hispaniolensis (a) and
Passer italiae (b) in Balcan peninsula

F i g. 1. Distribution of Hirundo rupestris (a) and
Carpodacus erytrinus (b) in Balcan peninsula

F i g. 4. Distribution of Cisticolla juncidis (a) and Hirundo daurica (b) in Balcan peninsula

F i g. 3. Distribution of Hippolais pallida (a) and Phylloscopus trochilus (b) in Balcan peninsula

F i g. 6. Distribution of Picedula hypoleuca (a), Ficedula semitorquata (b) and Ficedula albicollis (c) in Balcan peninsula

F i g. 5. Distribution of Streptopelia decaocto (a) and Oenanthe hispanicus (b) in Balcan peninsula
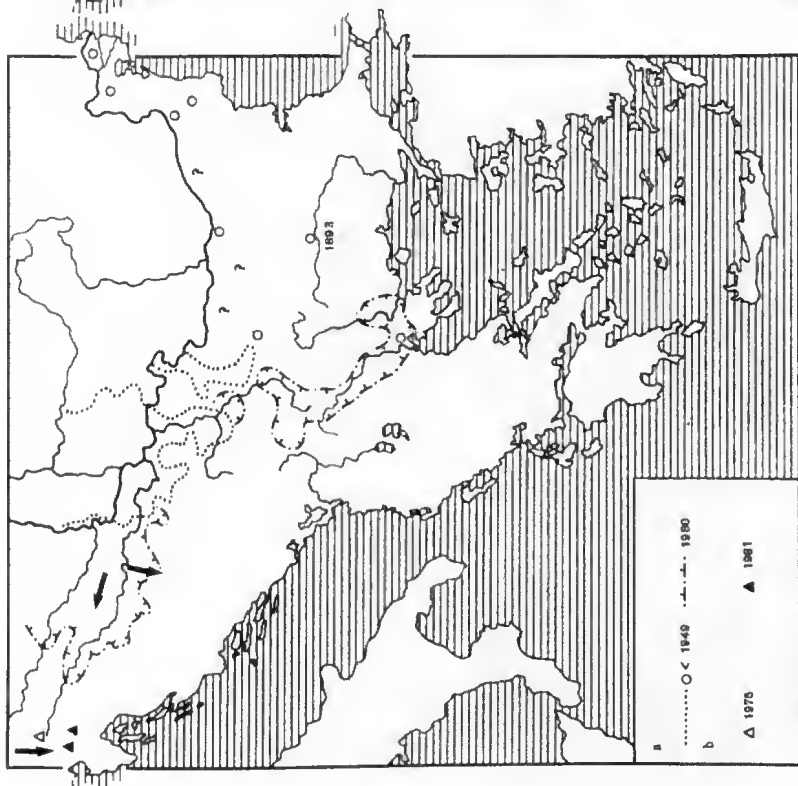
F i g. 7. Distribution of Corvus frugilegus (a) and Turdus pilaris (b) in Balcan peninsula
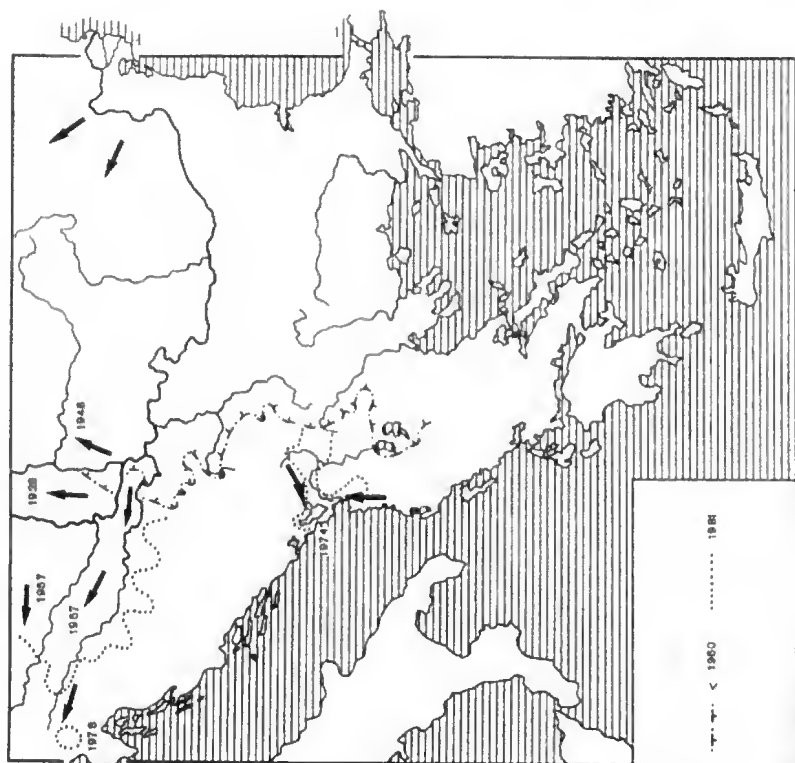
F i g. 8. Distribution of Dendrocopus syriacus in Balcan peninsula

The following changes in the ecological position more often lead to the expansion of bird areas in Balkan Peninsula:

1) Instillation of gardens and planting of separate fruit trees into entire steppe landscapes. This process led to the penetration of Streptopelia decaocto and Dendrocopus syriacus into the Central Europe.

2) Felling of forests, ploughing up of virgin soil and formation of a forest-steppe landscape: Corvus frugilegus, e.g.

3) Laying out of parks and planting of the groups of trees in steppe and semi-desert landscapes: Passer hispaniolensis.

4) Destruction of bushes and trees on stony slopes of mountains and gorges: Oenanthe hispanica, Hirundo rupestris.

5) Opening of sand-pits and quarries in the centre of a forest landscape: Oenanthe hispanica.

6) Growing shallow of dense forest complexes, i.e. increase of a number of borders: Phylloscopus trochilus, Ficedula hypoleuca, Carpodacus erythrinus.

7) Decrease in a number of beasts and birds of prey which leads to an increase in a number of Turdus pilaris.

8) Less destraction of singing birds by a man - e.g. Passer italiae in Yugoslavia.

References

Acrocephalus, 1980-1982, 1-12.
Larus, 1947-1980, 1-32.
Matvejev S.D. La distribution et la vie des oiseaux en Serbie. Academie Serbe des Sciences, monographie 161. Beograd, Reisers Ornis Balcanica, 1950, V.
Matvejev S.D. Survey of the Balkan Peninsula Birds fauna. I pt. Piciformes et Passeriformes. The Serbian Academie of Sciences and Arts, monography 491. Beograd, 1976.
Patev P. Birds of Bulgaria. Zoolog. Institute and Museum Bulg. Academy of Sciences. Sofia, 1950.
Reports of the Zoolog. Institute and Museum Bulg. Academy of Sciences. Sofia, 1951-1971, 1-33.
Reiser O. Ornis Balcanica. Wien, 1896-1939, I-IV.
Vasić V.F. Zbornik Priopćenja, Prvi kongres biologa Hrvatske. Zagreb-Poreč, 1981.

# DENSITY REGULATION IN BIRD POPULATIONS

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TERRITORIAL BEHAVIOUR AND THE LIMITATION OF BIRD POPULATIONS

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# TERRITORIAL BEHAVIOUR AND THE LIMITATION OF BIRD POPULATIONS

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## INTRODUCTION

It is widely accepted that selection on behaviour operates at the individual rather than at the population level and that territorial behaviour, especially territory size, varies in relation to the environment so as to maximise the fitness of the individual (Davies, 1980). This paper discusses the hypothesis that the consequence of this may adjust density to variations in environmental resources.

The definition of territory as a defended area will be used here. It is useful to separate two components; attachment to a site and aggressive behaviour shown toward conspecifics around the site. The maintenance of mutually-exclusive areas with rigidly defined boundaries, emphasised by some authors, does not seem necessary to the ideas presented here.

The aim of this paper is to consider the effects of territorial behaviour on population density by asking three questions:

a) can territorial behaviour limit population density?

b) if so, does the behaviour vary with environmental resources so as to change density in relation to these resources and

c) if so, how exactly does the behaviour determine the particular density achieved in a given environment?

All of these questions have been widely discussed elsewhere (e.g. Brown, 1969, Davies, 1978; Klomp, 1972; Patterson, 1980). I will deal only briefly with arguments and examples which appear elsewhere and will concentrate on recent work on the Crow _Corvus corone_ and _C.cornix_ at Aberdeen, Scotland.

## CAN TERRITORIAL BEHAVIOUR LIMIT POPULATION DENSITY?

Watson and Moss (1970) proposed criteria for testing behavioural limitation of breeding populations. The most important of these for this discussion are (a) that a substantial part of the population is excluded from breeding, (b) that the excluded individuals are physiologically capable of breeding and (c) that the established residents are not using up the whole of a resource (otherwise the resource itself would be limiting). The classic test of criteria (a) and (b) is to remove established territorial residents to find whether they are replaced by others, which must previously have been excluded by the residents. A large number of such removal experiments, demonstrating the presence of surplus or floater individuals, are reviewed by Brown (1969) and Davies (1978) and need not be detailed here.

Charles (1972), in addition to removal experiments, extended the breeding habitat of crows to create new opportunities for settlement. He created additional nesting habitat by erecting small trees in previously unoccupied tree-less areas. All the trees were occupied within a week by flock pairs which defended an area around them. Three of the pairs laid eggs in the first breeding season and one pair reared young. This experiment showed that additional nesting habitat was quickly occupied by previously non-territorial birds, which were capable of breeding when given the opportunity, thus satisfying Watson and Moss' (1970) criterion (b). Criterion (c) was also sa-

tisfied since, although only a single tree was sufficient for a pair to become territorial and breed, most territories contained an apparent surplus of trees. The resident pairs were not totally using up all available sites but were defending a surplus.

Charles' (1972) experiments thus confirm the well-established conclusion that territorial behaviour can limit density, by excluding individuals which are otherwise capable of occupying the habitat and of breeding successfully.

## VARIATIONS IN TERRITORIAL BEHAVIOUR WITH VARIATIONS IN RESOURCE LEVEL

To vary density in relation to the abundance of a resource, territory size should become larger at lower resource levels and smaller at higher levels. There is good evidence of this in several species, e.g. Sunbirds Nectarinia reichenowi (Gill, Wolf, 1975), Red Grouse Lagopus lagopus (Watson, Moss, 1980) and Davies (1980) discusses several examples in detail.

However, Spray (1978) has suggested that these are all species with short-term territories and that many are migrants, so that the territorial mosaic is frequently set up anew. Knapton and Krebs (1974) showed that simultaneous removal of all the territorial residents in an area led to resettlement at a higher density with a new system of boundaries, whereas single removals resulted in exact replacement with the same boundaries and no increase in density. Spray (loc. cit.) suggested that long-term territory systems, in long-lived species which are territorial throughout the year, will tend to have only occasional replacements of single territorial pairs. Change in density is unlikely since it could occur only if two pairs occupied one vacancy or if neighbouring residents expanded to fill it. There have been few studies of this type of territory. Harris (1970) has shown stability in territory size in Oystercatchers Haematopus ostralegus and studies of the Tawny Owl Strix aluco (Southern, 1970; Southern, Lowe, 1968; Hirons, 1976) have shown that, although territory size varied between areas and between habitat types, there was no change with very considerable variations in food abundance.

Crows also are long-lived species with long-term territory systems, defended throughout the year, which also should not change with short-term fluctuations in food abundance. Spray (1978) tested this experimentally, using the same study area as Charles (1972), by giving additional food to some territorial pairs. These spent significantly less time foraging and decreased the size of their range (relative to control pairs) but did not change in agressiveness or reduce the size of the area defended against non-territorial intruders.

This seems functional, since in such species an individual which reduced the size of its defended area in response to a short-term increase in food abundance might find it difficult to increase the area again. Another selection presure on crows to maintain a permanent large area could be intraspecific predation by the flock crows, which Charles (1972) found to be the commonest cause of egg loss. Breeding pairs may require a wide zone around the nest, to allow them to intercept an intruder flying from the boundary. This argument could be extended to other predators in which there is a risk of intraspecific predation.

To conclude this section, there is considerable evidence of change in territory size and consequent change in density, particularly in short-term territory systems. Long-term territory systems, however, seem to be resistant to change and there is a possibility that individuals may most of the time defend more of a resource than their immediate requirement.

THE DETERMINATION OF DENSITY

The territory systems which change in relation to changes in resource level raise the question of how precisely the change in behaviour achieves a particular density in a given situation. In the literature, the major emphasis is on the agression of territory owners and the size of area which they take and defend. The suggestion is that more aggressive animals take larger territories, resulting in a lower density than if less aggressive individuals took smaller territories (e.g. in Red Grouse, Watson, Moss, 1980). However, the existence of another factor is strongly suggested by data from simultaneous versus successive settlement (Knapton, Krebs, 1974), from expansion of territorial residents into adjacent vacated areas (Krebs, 1971; Watson, 1967) and from the finding that territories can be smaller than would be predicted from the aggressive behaviour of the owners (Patterson, 1965, 1980). This factor, operating against the aggressiveness of territorial residents, is likely to be the persistence of subsequent potential settlers. During settlement, as density increases and territory size decreases, new arrivals will be forced to settle closer to the centres of existing territories and so will suffer a higher level of aggression (Patterson, 1980). Further settlement should cease when the likelihood and severity of attack in boundary areas becomes sufficiently high to prevent potential settlers from staying for long enough to form an attachment to the area. The final density will thus be determined by the persistence and aggression of late arrivals and the non-territorial section of the population, in relation to the aggressiveness of the first settlers.

A problem in testing this hypothesis is how to measure the postulated behaviour of potential settlers. This may not be the same as territorial aggressiveness and it may not be possible to compare the two quantitatively. Charles (1972) used an experimental approach by manipulating the aggressiveness of potential settlers using testosterone implants and showed that the more aggressive birds were able to establish territories in areas where they had previously been excluded by the residents. This provides some evidence to support the hypothesis that final territory size and density is the result of a balance between the aggressiveness of the first territorial residents in an area and the persistence and aggressiveness of potential further settlers. The remaining problem is how this system could operate to vary density between habitats and between years.

One possibility is that variations in territory size and density, particularly between years, result mainly from differences in the inherent aggressiveness of the animals, both territorial residents and non-territorial individuals, as suggested in the Red Grouse (Watson, Moss, 1980). An alternative hypothesis is that different stocks of animals do not differ in their inherent aggressiveness but that they respond directly to the habitat, and particularly to the abundance of resources.

I have developed models to suggest how both hypotheses could vary density in relation to resource levels (Patterson, 1980) but data to test them are few. The studies of Red Grouse (Watson, 1967; Watson, Moss, 1980) supports the second. More data are clearly needed, particularly on how density is determined in long-term territory systems.

SUMMARY

There is considerable evidence, from removal experiments and from the addition of resources, that territorial behaviour can and does limit population density. In short-term territory systems there is also evidence that territorial behaviour varies with resource level so as to change density in relation to resources. Density may be adjusted through an interaction between the territorial aggressiveness of initial settlers and the persistence and aggressiveness of later arrivals and non-territorial individuals. Species with long-term territorial systems seem not to change their aggressiveness or territory size in response to short-term changes in resource abundance. In such species, any adjustment of territory size to resource level must be carried out over a long period and more study is needed of the mechanisms involved.

R e f e r e n c e s

Brown J.K. – Wilson Bull., 1969, 81, p. 293–329.
Charles J.K. – Unpubl. Ph.D. Thesis, University of Aberdeen, Scotland. Aberdeen, 1972.
Davies N.B. – In: Behavioural Ecology. An evolutionary approach / Eds. J.R.Krebs, N.B.Davies. Blackwell, Oxford, 1978.
Davies N.B. – Ardea, 1980, 68, p. 63–74.
Gill F.B., Wolf L.L. – Ecology, 1976, 56, p. 333–345.
Harris M.P. – J. Anim. Ecol., 1970, 39, p. 707–713.
Hirons G. Unpubl. D. Phil. Thesis. University of Oxford, England. Oxford,1976.
Klomp H. – Neth. J. Zool., 1972, 22, p. 456–488.
Knapton R.W., Krebs J.R. – Can. J. Zool., 1974, 52, p. 1413–1420.
Patterson I.J. – Ibis, 1965, 107, p. 433–459.
Patterson I.J. – Ardea, 1980,68, p. 53–62.
Southern H.N. – J. Zool. Lond., 1970, 162, p. 197–285.
Southern H.N., Lowe V.P.W. – J. Anim. Ecol., 1968, 37, p. 75–97.
Spray C.J. Unpubl. Ph.D. Thesis, University of Aberdeen, Scotland. Aberdeen, 1978.
Vines G. – Anim. Behav., 1979, 27, p. 300–308.
Watson A. – Nature, 1967, 215, p. 1274–1275.
Watson A., Moss R. – Ardea, 1980, 68, p. 103–111.
Watson A., Moss R. – In: Animal populations in relation to their food resources / Ed. by A.Watson. Blackwell, Oxford, England. 1970.

# COOPERATIVE BREEDING AND THE REGULATION OF NUMBERS

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## INTRODUCTION

The regulation of numbers in populations of birds has been studied most often in passerine species of Europe and in marine colonial species. In such cases non-breeding or surplus individuals may be difficult to monitor precisely, because they are inconspicuous or live elsewhere from the breeders. Cooperatively breeding birds differ from such species in that the surplus is readily visible. In addition, because of their habit of living in small groups, they may provide new perspectives.

The term, cooperative breeding, denotes a social system that is defined by the presence of helpers. A helper is traditionally defined as an individual who acts like a parent toward young that are not its own. Helpers are commonly non-breeders, but breeders may be helpers too, even simultaneously caring for their own and other young (Brown, 1970). The term communal breeding is frequently used as a synonym for cooperative breeding. Typically, a cooperatively breeding species lives in small groups of 2 to 25 - rarely more. Except in colonial cooperative breeders, which I shall not cover, these groups typically defend a group territory, are composed largely of the members of one family, have a stable composition from week to week, and are resident on their territory all year.

Cooperative breeders are interesting for the study of population regulation because the surplus birds are not expelled from their natal territories and may remain there for a long period, usually with their parents. This dramatic reduction of dispersal ameliorates the regulative effect of territoriality upon the population.

Most field studies of cooperatively breeding birds have not been designed to study population regulation, and few have been pursued for more than 6 years. One species that has been studied long enough to reveal something of its population fluctuations is the Mexican Jay (Aphelocoma ultramarina). I shall confine this presentation to the Mexican Jay because there is so little in the literature about population fluctuation in other cooperatively breeding species, and because a long term record is available for this species. We have just begun this analysis. I shall present here an overview of the first results.

## THE MEXICAN JAY

### General

The genus Aphelocoma belongs to the family Corvidae and ranges from Central America into Florida and much of western United States. All species are sexually monomorphic. The range of the Mexican Jay extends from central Mexico northward to just across the United States border in Arizona, where my observations are made, and to Texas.

## Habitat and Study Area

Ecologically the Mexican Jay is restricted to pine-oak woodland. In its range this habitat is largely montane. Consequently, its range has an insular pattern with isolated populations in many mountain ranges. My population is located in the Chiricahua Mountains, close to the Mexican border.

In each of the mountain ranges of this region, the Mexican Jay occurs at elevations intermediate between the higher, coniferous forests inhabited by Steller's Jay (Cyanocitta stelleri) and the desert srub that is inhabited by the Scrub Jay (A.coerulescens).

This pine-oak zone supports several species of oaks (Quercus spp.), and three are common on my study area. Mexican Jays harvest and store large numbers of acorns, competing for this crop with acorn woodpeckers (Melanerpes formicivorus).

Within this mountain range we located our study area in Cave Creek Canyon, at an elevation of 1,610 m in a broad basin.

Each bird is given a unique 6-digit number that corresponds to its color band combination. Using these "names" information on age, origin, movements, measurements, unit composition, reproduction, dominance, and genetic relatedness may be readily obtained for any individual or designated group or cohort of individuals from our computer files.

## Social Organization

The Mexican Jay is a social species. In 1963, using color-banded birds, we showed that the Mexcian Jay lives in flocks that are stable, territorial groups that behave as single social units (Brown, 1963). In this paper,therefore, the words flock, group and unit are used interchangeably as they apply to Mexican Jays.

In a survey of 38 units in Cave Creek Canyon in 1975, unit sizes varied from 5 to 15 and averaged 9.6 in June and 11.3 in August, after reproduction. Average flock size on our study area has varied yearly from 6.7 to 16.5(Fig.2).

By 1971 we had six units colorbanded and their territories mapped.Because the territories are held by groups, loss of even two to three birds does not usually cause a change in borders. Consequently, territory locations, sizes, borders, and numbers are exceedingly stable. Some borders have been stable since 1969. Consequently, our unit of study for purposes of charting population density, is defined primarily in terms of these flocks and secondarily in terms of area. Our population is the sum of the members of six flocks from 1971 to 1978. In 1979 a seventh group, composed largely of emigrants from the six original flocks, established a small territory in the middle of the study area, surrounded by the six previously studied units. Therefore, from 1979 to 1983 the population is defined by these seven flocks. The total area has increased 9 percent, from 155 to 168 ha since 1979.

All data on population numbers and fractions in this paper are from tallies taken in May and June of each year. All birds known to be alive on the study area on May 1 were counted. All were members of one of the six or seven units.
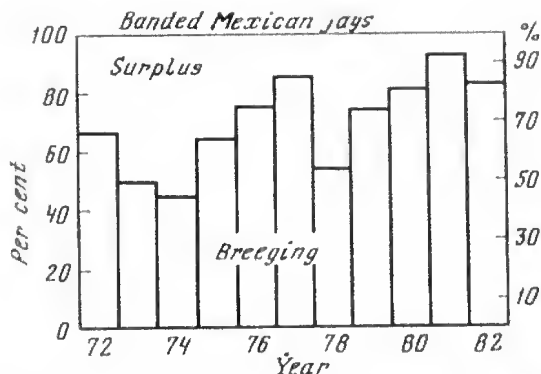
F i g. 1. The surplus population of Mexican Jays on 1 May. Data are for birds from the preceding year class or older. Birds of the year are not included. Percentage breeding was estimated for the banded birds only. The percentage of birds not banded ranged from 17% at the beginning to zero in 1982
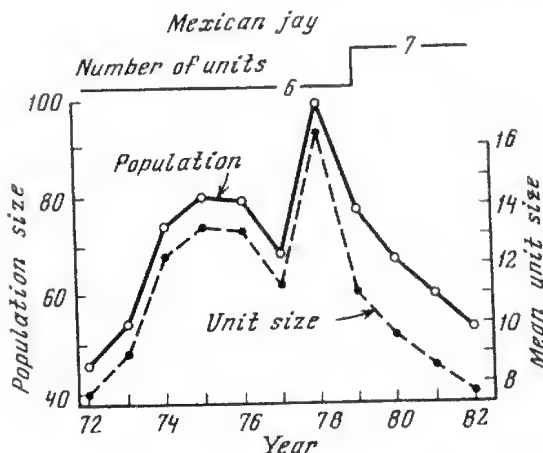


F i g. 2. Yearly variation in population size is reflected closely by variation in average unit size. The number of units on the study area varied only from six to seven

Plural Breeding

Unlike many cooperative breeders the Mexican Jay commonly has two or more females breeding within a single social unit, a condition known as pluaral breeding.

Table 1 shows that even when only successful nests are counted, plural breeding occurs in every flock and almost every year.

In this respect the Arizona population of the Mexican Jay differs from the Scrub Jay and possibly from the Texas population of the Mexican Jay. Since many offspring breed in their natal territory in the presence of their parents (Brown, Brown, 1980), the hazards of finding a new territory are reduced.

776

Table 1. Number of successful nests per unit in six social units of Mexican Jay from 1971-1978 and seven units from 1979-1982. Data are the numbers of nests in each unit each year from which young were fledged

| Year | TK | CO | HI | SW | BY | US | RC | Total |
|------|----|----|----|----|----|----|----|-------|
| 1971 |    | 1  | 0  | 1  | 1  | 0  | 0  | 3  |
| 1972 |    | 1  | 1  | 2  | 2  | 1  | 1  | 8  |
| 1973 |    | 1  | 1  | 2  | 2  | 1  | 1  | 8  |
| 1974 |    | 1  | 0  | 1  | 1  | 0  | 1  | 4  |
| 1975 |    | 1  | 1  | 2  | 2  | 1  | 0  | 7  |
| 1976 |    | 0  | 1  | 2  | 0  | 0  | 0  | 3  |
| 1977 |    | 1  | 3  | 2  | 3  | 2  | 1  | 12 |
| 1978 |    | 4  | 3  | 2  | 2  | 2  | 1  | 14 |
| 1979 | 1  | 1  | 3  | 1  | 0  | 3  | 1  | 10 |
| 1980 | 2  | 2  | 1  | 2  | 0  | 1  | 0  | 10 |
| 1981 | 1  | 3  | 1  | 3  | 3  | 2  | 1  | 14 |
| 1982 | 2  | 2  | 2  | 2  | 1  | 1  | 2  | 14 |

## THE SURPLUS

The surplus population in Mexican Jays is large and varies greatly from year to year. Fig.1 shows that the percentage of the population known to be breeding in a given year varied from 45 to 93. Those not breeding, in all likelihood, aided in care of the breeders' young. Furthermore, breeders whose nests fail revert to feeding nestlings at other nests. Therefore, the surplus fraction constitutes a minimum estimate of the fraction of the population acting as helpers.

In Mexican Jays, as in other cooperative breeders and unlike most territorial species the increment to the population remains in the preexisting territories. Roughly half of the individuals stay to breed in their natal territory and the remainder moves to a neighboring territory. In the entire study no move of more than 1000 m has been seen. No such moves have ever been recorded for this species. Few birds are seen that appear to lack territories. At most, such vagrants amount to 5%.

As a consequence of the failure of the non-breeders to leave pre-existing territories, the average size of the groups in these territories closely tracks the population level as shown in Fig.2.

The number of territories, in contrast, is much more stable.

## DELAYED BREEDING

In cooperatively breeding birds, some members of the population typically delay breeding. Mexican Jays of both sexes delay breeding when compared to the sympatric Scrub Jay, which may breed in its first year. As shown in Fig.3 no one-year olds have been recorded breeding, though some break twigs and carry them awhile. One-year olds have very light bills. Only 20% of two-year olds attempted breeding. At this age the light bill color diminishes, and the bill becomes all black by age 3. Not until the age of 4 does the percentage breeding level off. About 20-30% of breeding age birds may not breed on average. Adult levels of fledging success are not reached until the age of
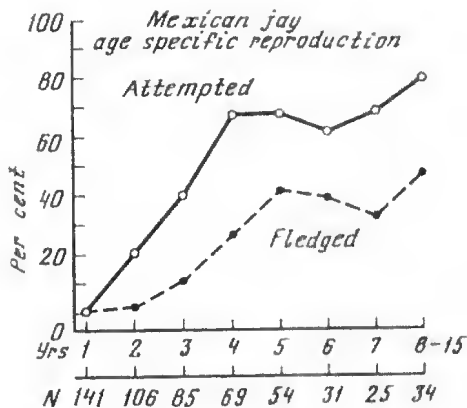
F i g. 3. Age-specific reproduction. The percentage of banded birds on the study area that attempted to breed at least by beginning to build a nest is shown by the upper curve. The percentage that fledged one or more young is shown by the lower curve. The sample is restricted to birds of precisely known age; they were banded as nestlings or year-lings. YRS - age in years. N - sample size

5 years. Because of such a long delay the maximum growth rate of Mexican Jay populations must be very small compared to other passerine species. This is compensated by a relatively high annual survival rate of about 80%. In respect to delayed breeding and survival Mexican Jays differ from most passerine species of the North temperate zone. Though there are exceptions, a relatively low population growth rate is characteric of many cooperatively breeding birds.

POPULATION FLUCTUATIONS AND AGE STRUCTURE

A conspicuous cause of yearly variation in numbers of Mexican Jays is the number of yearlings. A yearling in our study is a bird hatched in the preceding year who is roughly a year old on May 1. As shown    Fig.4    fluctuations in population size are largely determined by yearly variation in number of yearlings. As a consequence of the erratic production of yearlings the fact-
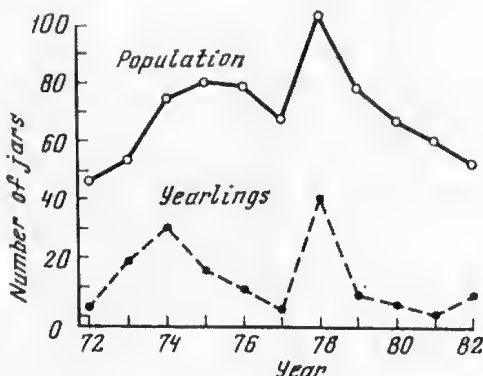


F i g. 4. Population numbers closely parallel the number of one-year-olds

ion of the population composed of yearlings varies greatly from year to year as shown in Fig.5. Because survival of yearlings and older birds is less erratic than the production of yearlings ( Fig.6 ), the latter factor has an overriding effect that pervades the entire age structure. The idea of a stable age distribution is a fiction for Mexican Jays. Figure 6 shows that two year classes, those of 1973 and 1977 ride through the years like a wave.
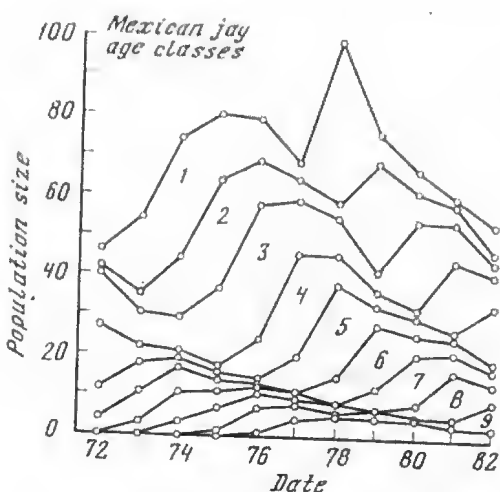


F i g. 5. The age structure of the population varied greatly from year to year. The curve above each of the ages in the figure shows the number of individuals of that age and older. The number in a given age class for a year is given by the vertical difference between the line above and the line below the indicated age. Data are for the entire population. Included are some unbanded birds and banded birds whose age is the stated age or older. The latter category declined steadily from 50% in 1972 to 15% in 1982
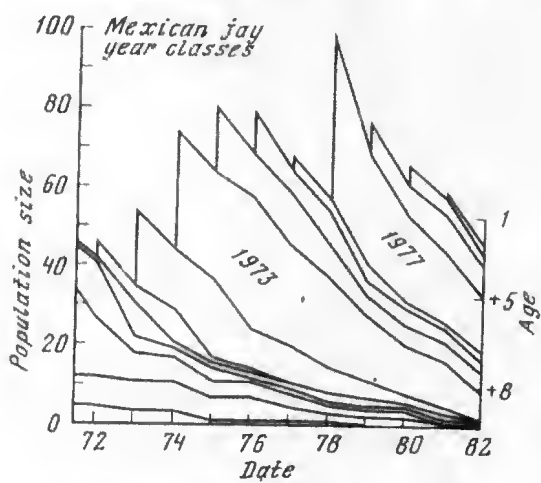


F i g. 6. Year classes in a population of Mexican Jays from 1972 to 1982. Data are as in Fig. 5

The number of yearlings is determined by the number of nestlings raised in the preceding year and by their survival. Each of these factors is highly variable as shown in Fig.7. The number of nestlings reaching banding age (14 days) varied from 8 in 1976 to 50 in 1978. The survival of these nestlings varied from zero in 1970 to 69% in 1973 and 1977. The greatest production of yearlings was achieved with moderately good production but excellent survival (1973, 1977 year classes). These conditions were relatively uncommon, but when they occurred they had a long lasting effect on the population. Consequently, increases in the population tended to be few (4) and large; decreases were more numerous (6) but smaller. Reproductive success in Mexican Jays is correlated with several climatic variables. The study area lies in an arid region whose precipitation and temperature vary widely. Table 2 shows the correlation of five measures of reproductive success and seven climatic variables over an 11-year period. The total numbers of nestlings and fledglings in the population each year are positively correlated with the amount of precipitation at the onset of the breeding season, in March and April. Additionally, the number of fledglings is positively correlated with the precipitation in the monsoon rainy season of the preceding July and August, the major rainy season. Winter rains (Sept.-Feb.) were not as important as the monsoon rains. Cold temperatures during the winter also have a negative effect on reproduction in the following spring. A similar pattern is found when reproductive success is divided by the number of birds of breeding age (defined here as three or more years old), as shown in Table 2.

Survival of nestlings is correlated with events in their first summer. Correlations of nestling survival with monsoon rainfall ($r_S$ = +0.60*) and with maximum temperature in the hottest month (June; $r_S$ = -0.60*) are significant.

The mechanisms of these effects are unknown, but it is reasonable to speculate that rainfall in the preceding summer affects the water table, the leaf growth of oaks and other trees, and the abundance of insects that utilize the affected vegetation. Cold winter temperatures might till overwintering insects and weaken potential breeders, thus reducing their reproductive success. Hot dry conditions shortly after fledging, in June to August, probably reduce the food available to juveniles.
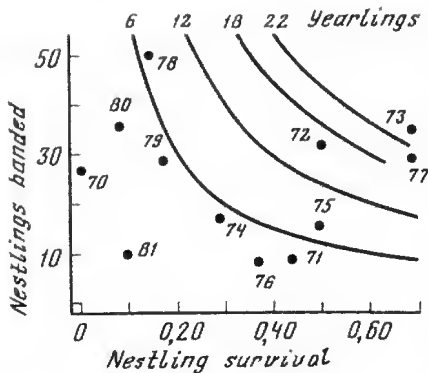
F i g. 7. Yearly variation in number of nestlings produced (Y-axis) combines with variation in survival of those nestlings (X-axis) to determine the number of yearlings in the following year. The number of yearlings is indicated by the contour lines, which connect points having the same number of yearlings designated above. The actual number of yearlings in the population is larger because of immigration. Each year class is designated by a number by its corresponding point

Table 2. Spearman rank correlation coefficients for 5 measures of reproduction and 7 climatic variables. All correlations discussed in this paper are based on Spearman rank correlation coefficients. On a one-tailed test these are designated * for $P < 0.05$ and ** for $P < 0.01$

| | Total Nestlings | Total Fledglings | Nestlings per Adult | Fledglings per Adult | Fledged Nest per Adult |
|---|---|---|---|---|---|
| Precipitation | | | | | |
| March-April | .53 | .55* | .54* | .59* | .68* |
| May-June | .17 | .41 | .38 | .45 | .41 |
| March-June | .45 | .63* | .68* | .74** | .75** |
| Preceding July-Aug | .39 | .67* | .40 | .58* | .66* |
| Preceding Sept.-Feb. | .27 | .45 | .40 | .53 | .35 |
| Temperature | | | | | |
| Coldest day of Preceding Winter | .56* | .68* | .44 | .49 | .49 |
| Coldest Monthly Ly Average Minimum in Preceding Winter | .72* | .63* | .64* | .62* | .73** |

Density-dependent effects on these measures of reproduction were not detected, with one exception. The number of nesting attempts was possitively correlated with the number of jays three or more years old, as would be expected (males, $r_S = 0.85**$; females, $r_S = 0.79**$). Some negative effects at higher densities were noted, however, on other factors. The number of fledglings per nest when restricted to those nests that fledged young was negatively correlated with the number of three-or-more-year-olds (males, $r_S = -0.86**$; females, $r_S = -0.66**$) but not with the number of yearlings ($r_S = 0.45$).

There appear to be some density effects on survival too, but these are significant only for yearlings ($r_S = -0.77**$ with average unit size; $r_S = 0.70*$ with population size).

SPACING, DISPERSAL, AND DISPERSION

Group territoriality in the Mexican Jay assures that areas suitable for permanent residence rarely become available. Although individuals are free to disperse and explore to find suitable areas elsewhere, they rarely do. Of the western North American jays, Mexican Jays are the least likely to be found out of their usual breeding habitat (Westcott, 1969). Consequently, each group tends to fluctuate in size according to its own reproductive success.

Very productive flocks (e.g., SW) are genetic exporters; their offspring may be found breeding in the neighboring units. Unproductive units are gene-

tic importers that receive emigrants from productive areas. These spacing mo-
vements tend to even out the population dispersion pattern. Whether such
spacing movements cause a density-dependent depression of reproductive suc-
cess at times of high numbers is not known. This issue is complicated because
we cannot know what reproductive success the dispersing birds would have had
if they remained at home. Preliminary analyses suggest that Mexican Jays tend
to move from units with an unfavorable sex ratio to units with favorable ra-
tios. Therefore, many spacing movements may have the effect of increasing
overall population growth. Furthermore, theory suggests the possibility that
territorial spacing can optimize utilization of habitats of different quali-
ty, thereby maximizing population reproduction (Brown, 1969).

## CONCLUSIONS

Mexican Jays have a low capacity for population growth because of delayed
breeding, which lowers $r_{max}$. Their territoriality, combined with a low growth
rate and relatively stable adult survival might be expected to stabilize po-
pulation density. Nevertheless, density-independent effects on the production
and survival of young seem to be the predominant influences on Mexican Jay
populations.

## ACKNOWLEDGEMENTS

## R e f e r e n c e s

Brown J.L. - Condor, 1963, 65, p. 126-153.
Brown J.L. - Anim. Behav., 1970, 18, p. 366-378.
Brown J.L. - Am. Nat., 1969, 103, p. 347-354.
Brown J.L., Brown E.R. - Science, 1981, 211, p. 959-960.
Westcott P.W. - Condor, 1969, 71, p. 353-359.

# DENSITY REGULATION IN COLONIAL SEA-BIRD POPULATIONS

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## INTRODUCTION

The effects of density in relation to size of populations of animals are intimately linked with the classical concepts of population regulation operating through density-dependent factors. These density-dependent factors increase their effect as the density of the species increases. For example fecundity, adult survival rate or both may decrease at high densities resulting in total or partial stabilization of the density and hence the population size.

This concept is the opposite in effect of "social stimulation" or the so-called "Frazer Darling Effect" (Darling, 1938) where breeding success is claimed to be higher in larger or more dense colonies.

It is abundantly clear that many colonial sea-bird species nest at densities far in excess of those found in many other birds of a similar size. This is not the place or time to consider the advantages in colonial breeding; these are to be considered in another session of this meeting, but it must be noted that breeding at such high densities would appear to facilitate the transmission of diseases and if for no other reason, it must be expected that appreciable advantages also accrue to species breeding colonially.

I have taken a wide view of density regulation and considered its influence in the following six categories, particularly from the point of possible population regulation:

1. Regulation of density in colonies.
2. Regulation of densities outside of the breeding season.
3. Regulation of colony growth.
4. Regulation of formation of new colonies.
5. Regulation of spatial distribution and size of colonies.
6. Regulation in relation to feeding during the breeding season.

As a result of this survey, I will suggest that the classical density-dependent relationships between density of birds within colonies and associated mortality rates do not, in general, appear to operate. They are, however, replaced by constraints on colony growth, formation of new colonies and the age at which birds succeed in breeding, which, together, control or regulate recruitment to the breeding population. These factors are not so much controlled by density in the breeding colony but by the size or density of the population in a wider area occupied by the species.

## 1. Regulation of density within colonies

Many species of sea-birds do not vary their nesting density in small and large colonies (particularly if density is measured by a "nearest neighbour" method), the distance between birds being determined by a short individual distance (e.g. Guillemot **Uria aalge**, Gannet **Sula bassana** and Sandwich Tern **Sterna sandvicensis**). The lack of considerable variation in density of many species suggest that density-dependent population regulating mechanisms connot be effectively operating through the small variation of densities found in colonies.
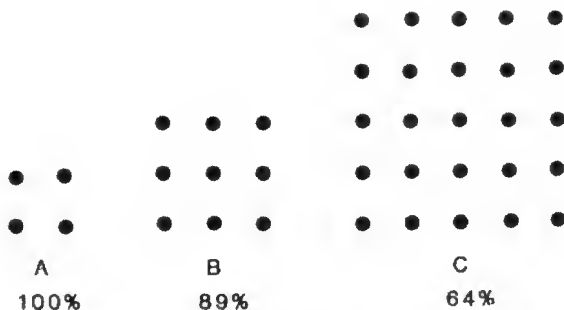
F i g. 1. A simple diagram to illustrats that, even when nests are evenly pla-
ced apart, a higher proportion of the birds are on the periphery in a small co-
lony and the birds, by this oriterion, could be regarded as being at a lower
density

Even though the nearest neighbour method may not show density differencss
between large and small colonies, there is an appreciable difference in the
numbers of pairs nesting on the periphery of small colonies whers the density
of their neighbours is lower than in a central site (Fig. 1). On classical
density-dependent ideas, it might be expected that these edge birds would
breed more successfully because of the lower density, but studies on Kittiwa-
kes, other gulls and penguins have shown the opposite effect with central
birds being appreciably more successful (even with no predation operating).

In other species there is some increase in the density of the breeding
birds as the colony increases in size. Such effects are obvious where Herring
Gulls Larus argentatus nest on rocky islets or sea-stacks where further ex-
pansion of the colony is limited. However in this species the nature of the
nesting terrain is even more important in determining nesting density. On
flat, rocky areas the nesting density reaches several times that on sand dunes
or on moorland. It would appear that on the last two mentioned there are re-
latively few suitable nest sites whilst the irregular nature of rocky islands
provides many potential nesting places.

Between 1972 and 1981, the Nature Conssrvancy Council reduced the numbers
of Herring Gulls breeding of the Isle of May, Scotland from about 20,000 pairs
to some 3,000 pairs. Ths reduced numbers bred over almost the same area as was
used in 1971 so that the density of nesting birds was reduced by about 5-6
fold. Differences in the breeding biology could be attributed to the reduct-
ion in nest density or the overall decrease in birds nssting in the arsa. Egg
size increased as did the sizs of the breeding birds (breeding success could
not be measured as clutches were destroyed in most areas). Recruitment took
place at a younger age and the extent of philopatry increased, presumably be-
cause of the reduced competition for nest sites (Coulson, Duncan and Thomas,
1982). Despite these effects acting against the species in 1971 (prior to the
onset of culling), the population had bsen rapidly increasing.

Kittiwake colonies also show increase in density as a colony grows but much
of the recruitment goes in expanding the limits of the colony. The maximum
density of nests in a Kittiwake colony is determined by the geology of the
cliffs and the density of ledges and this is the main source of the consider-
able variation in nest density found between colonies (Fig. 2).

**Nests within 0.8m radius**
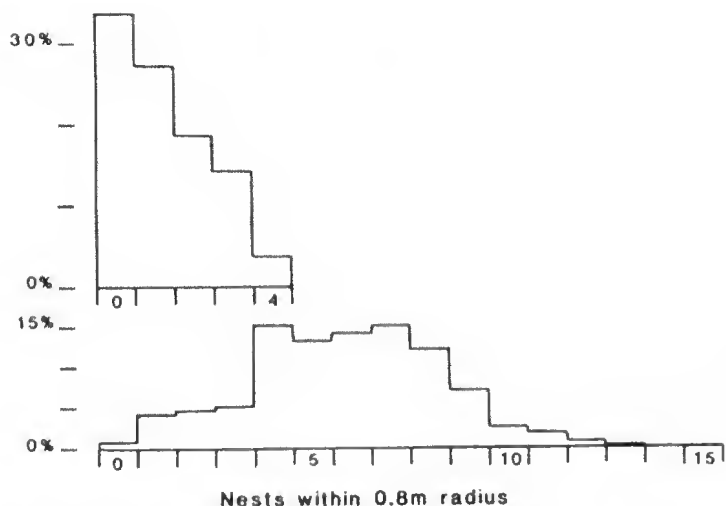
F i g. 2. The density of nests in two contrasting Kittiwake <u>Rissa tridactyla</u> oolonies. The upper diagram is of the colony at Dunstanburgh, Northumberland and the lower one is of Marsden Rock, Tyne and Wear. Density has been measured by taking the number of other nests in 0.8 m radius around each nest in the colony and plotting the values as a percentage frequency in each density class. Note that all Kittiwake colonies have low density areas but vary in the frequenoy distribution and particularly in the high density areas. This is mainly caused by the numbers and length of ledges on the cliff face

## 2. Regulation of colonial sea birds outside of the breeding season

In most sea-bird species, the density of a particular species is much reduced during the non-breeding part of the year compared with the breeding season. In some species e.g. Puffin <u>Fratercula arctica</u>, Fulmar <u>Fulmarus glacialis</u> and Kittiwake, oceanic areas are exploited to a much greater extent at this time and accordingly the density of feeding birds is typically extremely low except at favourable sites. Further, there is often extensive mixing of populations which breed many hundreds and even thousands of kilometers apart. Kittiwakes from Arctic Russia and Norway mix with those from British colonies and those breeding on the east coast of North America. The density of only a small number of species is increased in the winter months. The Herring Gull and Black-headed Gull <u>Larus ridibundus</u> are examples where increased winter density occurs. In N.E. England the wintering "population" consists of local breeders, birds which have moved south out of Scotland and numbers of Scandinavian or Baltic breeding birds. Whilst in these two gull species, there is reason to believe that density regulation does occur at winter feeding sites, this may be exceptional for colonial sea-birds and I do not propose to consider this further at this time.

In general, mixing of populations and the extremely low density of pelagic sea-birds which have spread beyond the limits created by their attachment to breeding sites makes it unlikely that appreciable density related effects operate in the winter months.

F i g. 3. The growth of the Kittiwake <u>Rissa tridactyla</u> breeding population at Marsden, Tyne and Wear, in comparison with that in individual colonie. The log plot of the data represents the rate of growth by the steepnese of the line

F i g. 4. The presentation ie the same as in Fig. 3, but shows growth in 3 sections of a colony (centre, sub-centre and edge). The top line is the rate of change in a nearby colony which was nearly eaturated and the figure illustrates the variatione of growth rates which can occur in an area where young are recruited from a common pool

### 3. Regulation of growth in coloniee

In many epecies of sea-birds which are increasing in numbers, the pattern of increaee within colonies differs from that of the population ae a whole. Some colonies grow much more rapidly than others. Since potential recruite are not limiting, presumably certain characterietics of the colony structure restrain colony growth. Neleon (1978) has ehown that very small Gannet colo-niee (e.g. Saltee and Bempton) grow extremely slowly until they reach a thres-hold number after which growth is rapid, even exceeding the rate in large, eetablished colonies.

In a study of Kittiwake colonies within the eame limited area, the numbers in the area as a whole increaeed at a constant rate, but the rate of growth of individual coloniee ehowed a progreseive slowing with age (or eize)(Fig.3), suggeeting that the structure of growing coloniee becomes progressively less attractive to recruits. Theee differencee can also be eeen eimultaneously in different parte of the same colony (Fig. 4). Since philopatry is not highly

786



F i g. 3. The growth of the Kittiwake <u>Rissa tridactyla</u> breeding population at Marsden, Tyne and Wear, in comparison with that in individual colonie. The log plot of the data represents the rate of growth by the steepnese of the line

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T a b l e  1. Recruitment and annual growth in three parts of a growing
Kittiwake colony and in a nearby colony which has no room for further growth.
Based on data in Figure 4 and assuming a 20% annual adult mortality

|  |  | Recruitment | |
|  |  | Average | Percent in growth |
|---|---|---|---|
| Edge | increase | 8.75 | 85.4% |
|  | recruits | 10.25 |  |
| Sub-centre | increase | 9.43 | 74.2% |
|  | recruits | 12.71 |  |
| Centre | increase | 8.63 | 59.0% |
|  | recruits | 14.75 |  |
| Nearby "full" colony | increase | 5.60 | 9.9% |
|  | recruits | 56.75 |  |

developed in the Kittiwake, these differences can be interpreted as indicat-
ing selection by the young recruits. I have examined this further by consider-
ing the total recruitment to three parts of a growing colony and to a nearby
colony which was no longer expanding. From the number of breeding pairs
(Fig. 4) the annual increase can be easily determined. To this total I have
added the numbers needed to replace adult mortality, assumed to be 20%, giving
the total recruitment. Table 1 summarizes the results. Despite the difference
in growth in the three sub-sections of the colony, total recruits were simi-
lar but the proportion of recruits needed to replace adult mortality was less
at the edge so that a much higher proportion of the total recruitment was al-
located to increasing the number of breeding pairs. As a colony increases in
size, more recruits are needed to replace adult mortality and proportionally
less contribute to colony growth. (It must be emphasized that the young pro-
duced in a colony of Kittiwakes contribute only a small proportion of the
recruits to that colony; most come from other neighbouring colonies.)

The young of many sea-bird species do not find it easy to recruit into a
colony. Near-saturation exists in the centre of the colony and new places
appear there only as a result of adult mortality. At the edge of the colony
only a narrow area can be used by recruits (apparently because they need sti-
mulation). This often results in a large number of birds capable of breeding
but failing to obtain and retain suitable sites. This problem of finding a
place to breed is similar to that of forming new colonies.

## 4. Regulation of the formation of new colonies

Fulmars are well known for their ability to colonize new areas. The whole
of the expansion around Britain is characterised by the formation of many new
breeding groups. This is in marked contrast to many other sea-bird species
where there is clearly considerable difficulty or resistance to forming new
colonies. For example, between 1909 and 1969, the North Atlantic numbers of

the Gannet increased threefold but the number of colonies only doubled (Nelson, 1978). Similarly the expansion of the Kittiwake in Britain between 1900 and 1922 resulted in the doubling of their numbers but no new colonies were formed. Only when the population growth continued further were new colonies formed (Coulson, 1963).

It is evident that solitary breeding does not occur in many sea-bird species and a group of individuals have to collect together before breeding is successful. Typically, new Kittiwake colonies are formed by 30-100 birds but in the first year that breeding takes place only 5-10 pairs actually build nests and lay. Similarly breeding is mainly unsuccessful in the Gannet until about 20 pairs are established in a new colony (Nelson,1978).

This difficulty in establishing new colonies is important since it is obviously not easy for birds which fail to obtain a suitable site in an established colony to move and set up a new colony. This results in an appreciable number of birds of potential breeding age failing to do so, thus increasing the mean age at first breeding.

## 5. Regulation of spatial distribution and size of colonies

Some species of sea-birds breed in colonies which contain hundreds of thousands of individuals but others clearly do not build up such large colonies although they are as numerous. For example the two species whose nesting colonies are shown in Fig. 5 show a marked contrast in the frequency and size of their colonies. The Gannet has few colonies, many of which are large and the British population.in 1969 was about 138,000 pairs. In contrast the Cormorant has a British population of just over 8,000 pairs but nearly 9 times more colonies. The most obvious explanation of this difference is related to the ability of the two species to exploit feeding areas around the British Isles. Nelson (1978) believes breeding Gannets have a feeding range of about 320 km whereas Pearson (pers. comm.) considers that breeding Cormorant are restricted to a range of about 30 km. Obviously if the Cormorant is to exploit the potential feeding sites in Britain it must form many,small colonies. The food resources used by the Gannet can be exploited either by a small number of large colonies or a large number of small ones; and the species has selected the former strategy.

I have examined the relationship between maximum colony size and feeding range during the breeding season for 15 colonial sea-birds exploiting fish stocks around the British Isles. Species present in small numbers have been excluded as has the Razorbill Alca torda since I have no information on its feeding range. To avoid bias, I have taken the largest British colony for each species reported in the national sea-bird census carried out in 1969 (Cramp et al., 1974). The maximum feeding range (when rearing young) of each species has been taken from Pearson (1968 and unpublished data) with the exception of the Manx Shearwater where I have taken the range from Harris (1966) and the Gannet,from Nelson (1978).

The inter-relationship between feeding range and maximum colony size, is shown in Fig. 6 and the correlation is high. Perhaps the relationship is
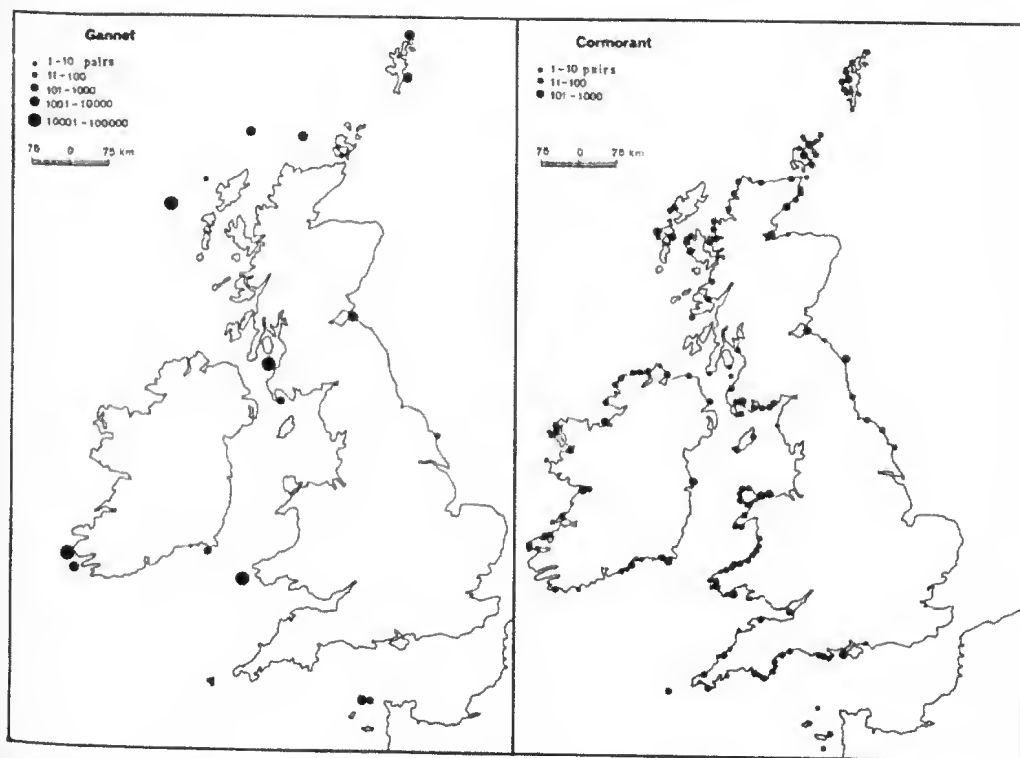
F i g. 5. The distribution of nesting colonies of the Gannet <u>Sula bassana</u> and the Cormorant <u>Phalacrocorax carbo</u> in the British Isles in 1969 (after Cramp et al., 1974). Note the few Gannet colonies compared to those of the Cormorant, despite the greater population of the former
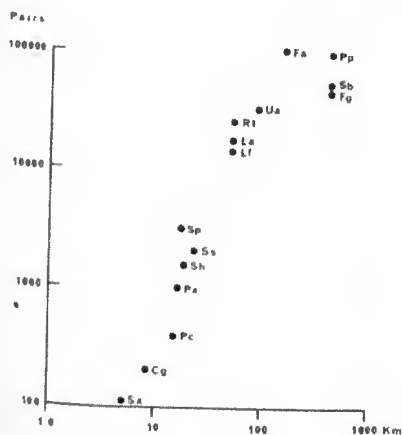


F i g. 6. The relationship between maximum colony size in the British Isles in 1969 and the individual maximum feeding range during the breeding season of 15 sea-bird species ( Fa-<u>Fratercula arctica</u>,Pp-<u>Puffinus puffinus</u>, Sb-<u>Sula bassana</u>, Fg-<u>Fulmarus glacialis</u>, Ua-<u>Uria aalge</u>, Rt-<u>Rissa tridactyla</u>, La-<u>Larus argentatus</u>, Lf-<u>L.fuscus</u>, Sp-<u>Sterna paradisaea</u>, SS-<u>S.sandvicensis</u>, Sh-<u>S.hirundo</u>, Pa-<u>Phalacrocorax aristotelis</u>, Pc-<u>P.carbo</u>, Cg-<u>Cepphus grylle</u> and Sa-<u>Sterna albifrons</u>)

obvious; it clearly suggests that sea-birds are attempting to utilize poten-
tial food resources. What is not clear, however, is why those species with
long feeding ranges opt for large colonies. The implication is that, provid-
ing food resources are adequate, there is an advantage in a large rather than
in several smaller colonies. Apart from the possible shortage of suitable
nesting sites in some species, advantages in forming one colony of, say,
100,000 pairs rather than five of 20,000 have not been considered previously.

## 6. Regulation in relation to feeding density during the breeding season

One of the implications derived from Figs. 5, 6 is that food and feeding
influence the size and perhaps the position of breeding colonies. The impli-
cation of food is of interest and begs the question "Can feeding bring about
the control of breeding numbers?". In simple terms, one is looking for an ef-
fect which causes food shortage in large colonies but not in smaller ones.
This leads to the question of whether sea-birds greatly reduce the stocks of
their food. It is difficult to believe that surface feeders and those which
dive just below the surface can exploit fish to the extent that they markedly
reduce the fish density even if the birds are present in large numbers. Diving
species can approach their foood supply more effectively. Furness (1978) has
estimated that the sea-bird populations may take up to 30% of the food supply
during a breeding season, but this is in regions of very high sea-bird numbers.

This is a field which needs more research. Apart from the direct interac-
tion between food and predator there is also the possibility of interaction
between feeding individuals, which is probably more intense in those species
with a short feeding range.


DISCUSSION AND SUMMARY

Too little is known about sea-birds in their wintering areas to be able to
comment with any certainty as to whether density regulation takes place at
this time. Many species are spread out to a greater extent at this time and
usually the density of individuals is much lower than during the breeding
season, when the birds are limited by the feeding range from the colonies.
Except in a few species, such as some gulls which accumulate at high densities
in some localities in winter, there may not be much density regulation out-
side of the breeding season. Since many species form mixed-population flocks
or groups, any regulation which does occur is unlikely to regulate the size
of the breeding populations.

In those see-bird species which nest at incredibly high densities, packing
closely together, there is little variation in nesting density and the densi-
ty in each species is determined by its characteristic individual distance.
The only source of variation is colony size and hence the proportion of birds
nesting at the periphery. Even in those species which show variation in nes-
ting density, much of this variation can be subscribed to variation in the
nature of the nesting area and the availability of nest sites.

Most sea-birds do not form colonies each of which is a closed population
and some recruitment takes place from the young reared in neighbouring colo-

nies. However there is a wide range of philopatry in sea-bird species which is particularly high in Gannets, Shags and Cormorants and low in Sandwich Terns.

It is clear that individual colonies do not usually regulate the density of sea-birds on an area but there is evidence that they exert a restraint on the growth of the breeding population in an area through the social conventions associated with recruitment. In effect, the social behaviour induces a shortage of nesting sites, although physically acceptable sites are in abundance (Coulson, 1971; Potts et al., 1980).

The relationship between maximum colony size and the feeding range of breeding birds suggests an interaction between food, the ability to exploit a food resource and the distribution of colonies. There is need for much more research in this field but here is a possible mechanism which could regulate the density of sea-birds feeding around areas used for breeding. Is it possible that sea-birds deplete their food supplies sufficiently to result in a feed-back which influences their survival or their breeding success. I find this difficult to envisage for surface feeding species and those which plunge just below the surface. So much of their potential food supply is out of reach at any one time that factors affecting the availability of food would appear to be more important. This restraint is less severe in deeper diving species. The model of Furness (1978) suggests that sea-bird colonies in northern Scotland were taking about 30% of the total fish production each year. This, in itself, does not deplete the available food within the breeding season to a major extent as the production is continuing throughout the breeding season. Simultaneously, however, large fish, marine mammals and man are also actively exploiting this production. Overexploitation of the stock will reduce the production and the most likely organism to do this is man. If sea-bird population sizes are determined by feed-back through the food supply, then man's fishing activities are going to have widespread effects in the next few decades.

R e f e r e n c e s

Coulson J.C. - Bird Study, 1963, 10, p. 147-179.
Coulson J.C. - In: Proc. Adv. Study Inst. Dynamics Numbers Popul. (Oosterbeek 1971). 1971.
Coulson J.C., Duncan N., Thomas C. - J. Anim. Ecol., 1982.
Cramp S., Bourne W.R.P., Saunders D. The Seabirds of Britain and Ireland. L.: Collins, 1974.
Darling F.F. Bird flocks and the breeding cycle. Cambridge: University Press, 1938.
Furness R.W. - J. Anim. Ecol., 1978, 47, p. 39-53.
Harris M.P. - Ibis, 1966, 108, p. 17-33.
Nelson J.B. The Sulidae: Gannets and Boobies. Oxford: University Press, 1978.
Pearson T.H. - J. Anim. Ecol., 1968, 37, p. 521-522.
Potts G.R., Coulson J.C., Deans I.R. - J. Anim. Ecol., 1980, 49, p. 465-484.

# THE EFFECT OF INTERSPECIFIC COMPETITION ON NUMBERS IN BIRD POPULATIONS

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## INTRODUCTION

Very few papers on interspecific competition in birds have considered if the competition  which was observed or inferred had any effect on the numbers in the population. The definition of interspecific competition, however, says that competition has a negative effect on all species-populations involved, as made explicit by its mathematical formulation (equation 1). This states that the growth rate of a population per unit time (dN/dt) is reduced by the presence of individuals of the same species (intraspecific competition) and by the presence of individuals of another species (inter specific competition)

$$\frac{dN_1}{dt} = r_{m_1} \cdot N_1 \ (1 - \frac{N_1}{K_1} - \alpha_{1j} \cdot \frac{N_j}{K_1}) \tag{1}$$

i, j: species; N: population size; t: time; $r_m$ intrinsic rate of natural increase; $\alpha$ : competition on the per capita growth rate

$$r = \frac{1}{N_1} \cdot \frac{N_1}{dt} = r_{m_1} \ (1 - \frac{N_1}{K_1} - \alpha_{1j} \cdot \frac{N_j}{K_1}) \tag{2}$$

Using this approach it is clear that very few papers that talk about competition have really shown that interspecific competition takes place. For interspecific competition to be proven the author must provide evidence that the population growth rate or the per capita growth rate of species i is reduced by the presence of species j, or is a function of the density of species j, and vice versa. If sufficient data are available zero-growth isoclines can be drawn.

Owing to the limited space I will not exhaustively review all bird papers on interspecific competition assessing them in the light of the above equations. Rather I will (1) expand the traditional equations based on the logistic model to a simple non-linear model, (2) provide some evidence that the per capita growth rate can be a non-linear function of population density in birds, (3) discuss some implications of this non-linear density dependence on the effect interspecific competition has, and (4) use data on Belgian Tits to illustrate some of the points made.

### ON NON-LINEAR DENSITY DEPENDENCE

Smith (1963) showed that in a laboratory population of water fleas the per capita growth rate was a non-linear function of population density. The same is true for some fruit-fly species (Ayala et al.,1973). In both these examples the relationship is concave. In reanalysing the Pheasant data from Protection island (Einarsen, 1945) a similar concave curve appears (Fig.1). As shown in the bottom part of the figure this is the result of the non-linear density dependence of recruitment[*]. The Lotka-Volterra equations (cf. eq. 1 and 2) are clearly inadequate to model these non-linear relationships.

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[*] Fowler (1981) has given examples of convex curves.
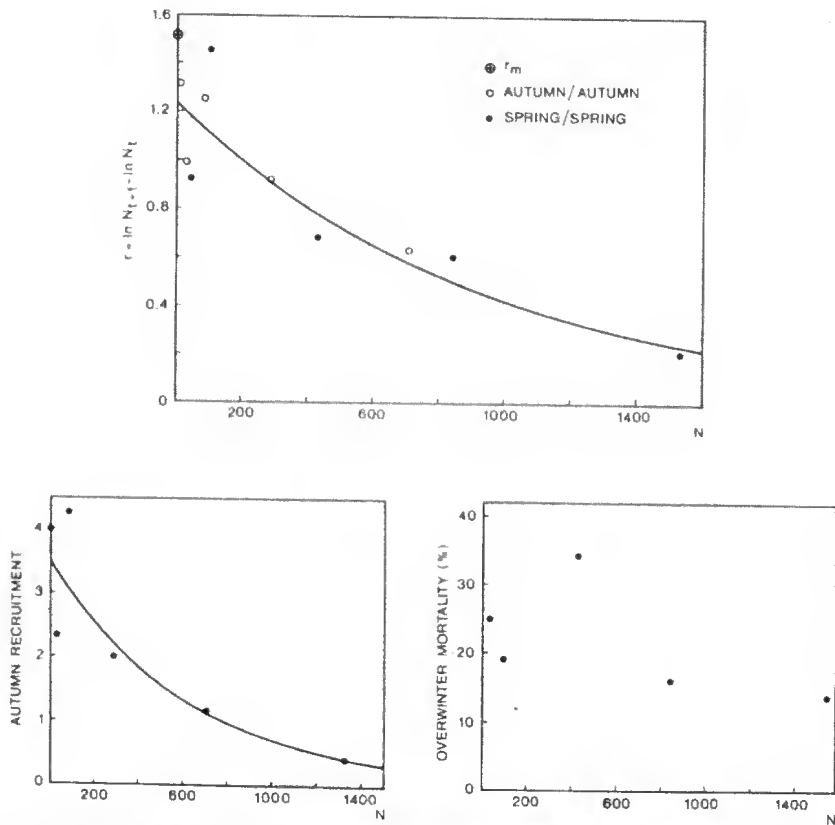
F i g. 1. Re-analysis of the Pheasant _Phasianus colchicus_ data of Protection Island (Einarsen, 1945) (see also text)

One of the more complete explorations of what mathematical model best described experimental results was made by Ayala et al.(1973). They considered twenty different models and selected the following one (equation 3):

$$r = \frac{1}{N_i} \cdot \frac{dN_i}{dt} = r_{m_i} \left(1 - \left|\frac{N_i}{K_i}\right|^{\theta_i} - \alpha_{ij} \frac{N_j}{K_i}\right) \tag{3}$$

One of the attractive things about this model is that the Lotka-Volterra equation is a special case for $\theta = 1$. As shown in Fig.2 the model produces concave curves ($\theta < 1$), convex curves ($\theta > 1$) as well as a straight line ($\theta = 1$). By introducing the power $\theta$ the model implies a non-linear intraspecific effect, but a linear interspecific effect.

I am fully aware of the fact that this model has its shortcomings: it does, f.i. not take into account the Allee effect. I will nevertheless use it in the remaining part of this paper. Any conclusions drawn remain at least qualitatively valid for other non-linear models.

It is important now to consider in what species $\theta$ would be large and in what species $\theta$ should be small. Gilpin et al. (1976) explored this and concluded that in stable environments high values of $\theta$ would be favoured, whereas low values would be optimal in unstable environments. In a different jargon this means that low values of $\theta$ ($< 1$) are typical for r-selected species whereas large values ($> 1$) of $\theta$ must be found in K-selected species.
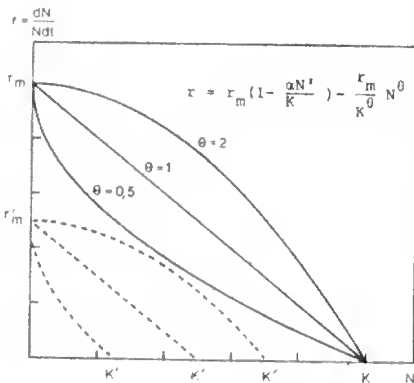
F i g. 2. Curves obtained for different values of θ using the model shown in equation 3. The full curves show the effect of intra-specific competition only on the per capita growth rate. All curves go from $r = r_m$, $N = 0$ to $r = 0$, $N = K$. The stippled curves include the effect of interspecific competition. They all start at $r'_m$ $(<r_m)$ but the value K' for $r = 0$ is determined by θ

In the bottom part of fig. 2 I have drawn the curves in which the effect interspecific competition has been added. We see that for large values of the new equilibrium value (K') lies rather close to the K-value in the absence of interspecific competition (for $\alpha_{ij} = 0$). For small values of $\theta$ however, the difference between K and K' is large. In fact the smaller the value of $\theta$, the larger the difference between K and K' becomes.

This model thus shows that r-selected species suffer heavily from interspecific competition, whereas K-selected species suffer only mildly.

Where do the birds now fit? Blusweiss et al.(1979) have shown that a close relationship exists between the intrinsic rate of natural increase $r_m$ and body weight over all animal groups. Although birds on the whole are K-selected species the maximal growth rate calculated from Blueweiss' formula can vary f.i. between 4.19 per annum for a 20 g bird (e.g. a Great Tit), over 1.51 per annum for a 1000 g bird (e.g. a Pheasant - this value is shown as $r_m$ in Fig.1), to 0.87 per annum for a 8500 g bird (e.g. an Albatross). Within the group of birds we therefore undoubtedly find species that are more r-selected (the small songbirds with large clutches, several broods per year and a high mortality rate) and species that are more K-selected (the large seabirds with a long delay in reproduction, a clutch of 1 and low mortality rates). If the model is correct I would expect concave curves for small songbirds, but convex ones for large seabirds, raptors, etc. Small songbirds exposed to interspecific competition would then strongly be affected, but the K-selected bird species would show only a slight numerical response to interspecific competition.

NON-LINEAR DENSITY DEPENDENCE IN THE BLUE TIT

Earlier I stated that in order to prove interspecific competition it is necessary to show that the per capita growth rate at a given density of a species varies inversely with the population size of the competing species. In Figure 3 I have plotted the per capita growth rate of different Blue Tit populations in relation to population density: the population "Zevergem" (16 ha, mainly oak) over the period 1959-1977, showing an inverse relationship between r and N and the points for a second area "Gontrode" (18 ha, mainly oak) for the years 1972-1976 lying very close to this line. As described by Dhondt, Eyckerman (1980) an experiment was performed in Gontrode resulting in a decrease of the Great Tit population size and an increase in the size of the
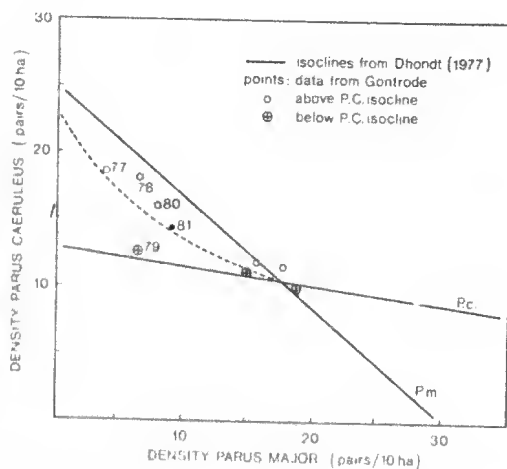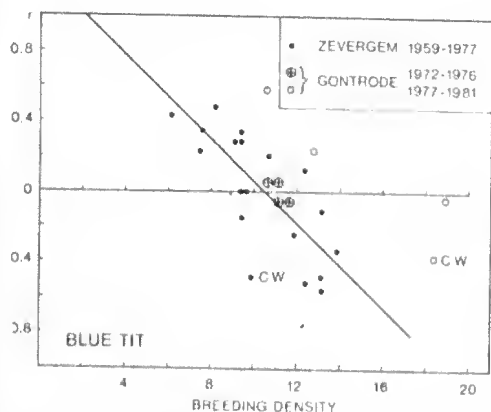
F i g. 3. Per capita growth rate in relation to breeding density (per 10 ha)
for different Blue Tit populations (see text)

F i g. 4. Blue Tit isoclines estimated after experimental reduction of Great
Tit population at Gontrode (see text)

Blue Tit population. The four points for the experimental years 1977-1981
all lie clearly to the right of the line for the normal years, including that
for the cold winter 1978-79.When Great Tit population size is reduced to about
8 pairs/10 ha, the per capita growth rate for the Blue Tit population incre-
ases and the Blue Tit equilibrium value (K) lies at around 16 pairs/10 ha, as
compared to 10.5 pairs/10 ha when the Great Tit population size is not mani-
pulated (Great Tit density: 16.2 pairs/10 ha). If we could exclude all Great
Tits the Blue Tit population size would increase still further. But to what
Level?

In an earlier paper (Dhondt, 1977) I have estimated the size of a Blue Tit
population in the absence of Great Tits using linear isoclines. I obtained a
K-value of 13 pairs/10 ha for the Blue Tit. In Figure 4 I have redrawn the
isoclines from that paper adding the points for the pre-experimental and the
experimental years in Gontrode. The four points for the pre-experimental years
fit the Blue Tit isocline for the other area quite nicely. The points for the
experimental years, with a reduced Great Tit population size, however, all 5
fall well above the linear isocline. I have therefore added to the figure a
curvilinear isocline for the Blue Tit (drawn by eye). This line is concave,
indicating a value of $\theta$ smaller than 1, as would be expected for this small
songbird. Such non-linear isoclines have also been found by Ayala et al.
(1973) for Drosophila spp.

CONCLUSIONS

Very few studies on bird populations show that through interspecific compe-
tition population size is reduced, or that growth rates are effected. Using a
mathematical definition of competition this implies that in these studies in-
terspecific competition has not been proven.

It is probable that in many cases the r/N is non-linear. The simple model

used shows that more r-selected species will suffer very heavily from inter-specific competition, whereas more K-selected species will be only mildly affected. It is quite concievable that in studies of such K-selected species it will be almost impossible to show an effect of interspecific competition even if it occurs. The new equilibrium level reached after the level of interspecific competition has been changed must lie closely to the old equilibrium level. Since the environment is never completely stable and micro-evolutionary changes could affect population parameters the original K-value will fluctuate so that the new equilibrium level could easily fall within the range of variation of the original one and no interspecific competition can be shown.

In the neighbourhood of the equilibrium level K the slope of the curve describing the r/N relationship differs for r- and K-selected species (with values of $\theta$ respectively $< 1$ and $> 1$). The steeper the line, the more rapidly the population will react to small disturbances from the equilibrium level. K-selected species, that have a steeper slope around K, should therefore react more rapidly to small disturbances than r-selected species, in which the slope is smaller (see figure 2). K-selected bird species normally have a delayed maturation period with a non-breeding population of subadult birds. Since these birds, even in subadult plumage, are often capable of breeding (see f.i. Newton,1980, for a review of birds in prey) there is a reserve population that makes it possible for such a population at equilibrium to react directly to, for example, an adult dying. In r-selected species, in which all birds breed in their first year, this non-breeding reserve is not available (or limited to one sex only), so that it is only after the next breeding season that losses can be replaced.

SUMMARY

The mathematical definition of interspecific competition states that for interspecific competition to occur it must have an effect on the numbers of all competing species. Using a model proposed by Ayala et al., which is a simple expansion of the Lotka-Volterra equations and produces non-linear curves to describe the r/N relationship it is shown that the effect of interspecific competition on r- and K-selected species is very different. The belgian Tit data are used to illustrate some of the points made.

R e f e r e n c e s

Ayala F.J., Gilpin M.E., Ehrenfeld J.G. - Theor. Popul. Biol., 1973, 4, p. 331-356.
Blueweiss L. et al. - Oecologia (Berl.), 1978, 37, p. 257-272.
Dhondt A.A. - Nature (London), 1977, 268, p. 521-523.
Dhondt A.A., Eyckerman R. - Ecology, 1980, 61, p. 1291-1296.
Fowler C.W. - Ecology, 1981, 62, p. 602-610.
Gilpin E.M., Case T.J., Ayala F.J. - Mathematical Biosciences, 1976, 32, p. 131-139.
Newton I. Population ecology of raptors. Berkhamsted, 1979.
Smith F.E. - Ecology, 1963, 44, p. 651-663.

# REGULATORY MECHANISMS OF NUMBERS IN BREEDING
# POPULATIONS OF MIGRATORY DUCKS

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A great number of laboratory experiments have shown the presence of densi-
ty-dependent regulation of numbers in various populations of animals. This
important phenomenon has been considerably less studied under natural conditi-
ons. Investigations on natural bird populations mainly deal with non-migrato-
ry territorial species (e.g. Dhondt, 1971; Kluyver, 1971; Boag et al., 1979;
Zwickel, 1980). We present here our main findings on regulatory mechanisms
(intrinsic control) of numbers in relatively small breeding populations of
exploited migratory ducks. Tufted Duck (Aythya fuligula) and Shoveler (Anas
clypeata) were chosen as the main model species.

Long-term investigations on the population ecology of migratory ducks were
carried out at the shallow overgrown coastal Engure Marsh, Latvia. Since 1961
nest counts and subsequent mapping were carried out annually on the islands
and some slough area. Almost all incubating females and newly hatched duck-
lings were trapped and ringed at the trial plots. Different trapping and ring-
ing methods were used (Lejins, 1964; Mednis, Blums, 1976; Mihelsons, Blums,
1976; Blums et al., 1983). During 21 year 42550 newly hatched ducklings of 13
species have been ringed. From these 790 incubating females were retrapped
the succeeding years, mostly as one-year-old birds during their first breed-
ing season, and 3340 random recoveries were received. Including retrappings,
about 6200 captures of incubating females were registered. At the same time
environmental changes in nesting habitats were registered and a number of me-
nagement measures were performed to improve the nesting habitats and to cont-
rol the predators.

The main method of analysis was the calculation of correlation coeffici-
ents between the indices of density and survival of young birds or adults.
Numbers of counted nests expressed as a percentage of a moving average (i.e.
deviation from moving average) were used as index of density. In our opinion
a moving average of the number of counted nests (for example from 3 years)
reflects to a certain degree changes in the carrying capacity of the nesting
habitate over a more prolonged period. It is extremely important to consider
these changes in population studies because number of breeding females (or
pairs) per area not always can be used as criterion of "biological density"
(see Mihelsons, 1980: 58). The random recovery rate during different periods
of life and the recruitment rate of young females to first nesting were used
as index of survival.

In two main species under investigation the same phenomenon has been obser-
ved, i.e. the self-regulation of numbers of nesting females (Mihelsons, 1976,
1980; Mihelsons et al., 1981a). First of all the self-regulation is expressed
by a change in mortality rate among the population members, mainly among young
birds, depending on variations in biological density in breeding periods. Com-
paring years with different density of the nesting population the post-hatch-
ing survival of young ducks increases with the decrease of density index
(Fig. 1).Calculation of correlation coefficients between the indices of densi-
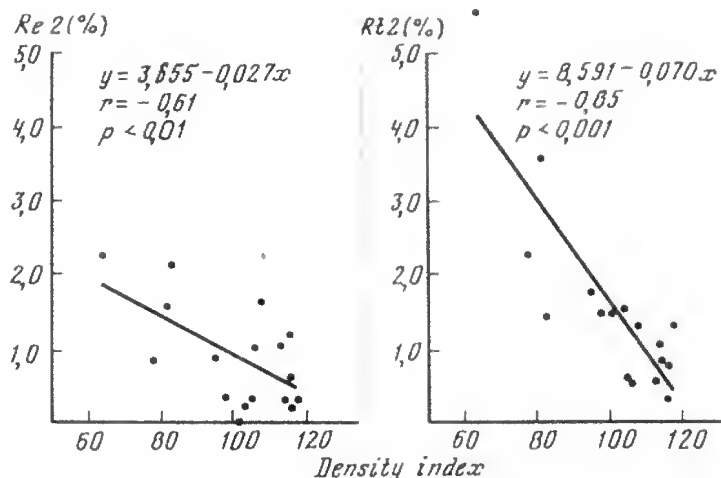
F i g. 1. Relationships between density index (see text and Table 2) and post-hatching survival of juveniles in breeding population of Tufted Duck on islands of Engure Marsh, Latvia, 1961-1979

Re2 - random recovery rate during second calendar year of life; Rt2 - recruitment rate to first breeding of one-year-old females. Both indices were calculated from the total amount of ringed one-day-old ducklinge of unknown sex in preceding year

ty and the random recovery rate of young birds in various autumn periods revealed that elimination of the excess amount of juvenile by shooting in the Tufted Duck occurs most intensively at the end of the breeding period and it is finished mainly before their departure from the natal area. In the Shoveler, the process of elimination goes on also during autumn migration and in the beginning of the wintering period. In juveniles of both species this process is almost completed at the end of the first calendar year (therefore we usually use the random recovery rate after the first of January of the second calendar year as an index of survival).

In the Tufted Duck there are facts suggesting that in the absence of hunting the surplus birds perished. We compared the recovery rate of birds ringed in the same years in two neighbouring populations - Engure Marsh (with autumn hunting) and Matsalu Reserve (without hunting) (Table 1). It was found that the random recovery rate of juveniles after departure from the natal area is the same for both areas (Fisher Test, $p > 0.05$) whereas the local recovery rate of the hunted population was much higher than that of the population without hunting. This means that autumn hunting on the Engure Marsh does not affect the size of the breeding population in the following year, as a large number of juveniles perished due to unknown natural causes whether the birds are hunted or not. Thus we suggest that natural and hunting mortality are not additive but mutually compensatory (Miheleone et al., 1981b, 1981c). A similar phenomenon was found for the Mallard (Anas platyrhynchoe) in North America by Anderson and Burnham (1976).

The physiological mechanisms depressing the vitality of birds at increased density have not yet been studied. High density probably increases the stress

T a b l e  1. Comparison of random recovery rate in Tufted Duck from two different populatione with (Engure Marsh, Latvia) and without hunting (Matsalu Reserve, Estonia), 1969-74

| Age and sex at ringing | Ringing place | N of birds ringed | N of recoveries (%) | |
|---|---|---|---|---|
| | | | During Ist calendar year < 60 km | During Ist and 2nd calendar year > 60 km |
| Pulli, indet. | Engure | 4171 | 257 (6.2) | 61 (1.5) |
| Pulli, indet. | Matsalu | 3754 | – | 48 (1.3) |
| Adult females | Engure | 604 | 14 (2.3) | 17 (2.8) |
| Adult females | Matsalu | 651 | 1 (0.2) | 18 (2.8) |

situation in birds through competition, by which they become more susceptible to unfavourable environmental conditione.

In the Tufted Duck we have investigated the demographic regularities causing a decreaee in the survival of ducklings in situations of high density. Thus, along with the increase in numbers the proportion of one-year-old local females and immigrants among the nesting females is also increasing. The survival of their ducklings is considerably lower than that of the older females (Mihelsons, Mednis, 1976; Mihelsons, 1980). The increase in numbers of nesting females usually causes prolongation of the breeding period. The overall post-hatching survival decreases, because the survival of ducklings from late clutches is inferior, as has been found in all duck species studied so far (Mihelsons et al., 1970). Both phenomena lead to a decrease in the survival of ducklings when the number of nesting females increases.

Long-term data on the Tufted Duck were collected not only on islands of the Engure Marsh where mass ringing was started in 1960, but also on slough area where ringing was started in 1966. Correlation coefficients between the density indices in separate limited marsh areas and the indices of post-hatching survival, i.e. the random recovery rate during the second calender year of life (Re2) and the recruitment rate of autochtonous females on the Marsh (Rt), were calculated. The results appeared to be different for the two survival induces. For Re2 the highest negative correlation coefficient of the survival in each separate area occurs with the index of density exactly from the same area where ducklings were hatched (Table 2). This allows us to suggest that in the initial stages self-regulation occurs mainly autonomically in each definite area, i.e. the survival of ducks during the first calendar year of life is affected especially by the increased density of nesting females at the limited hatching sites, more than by the density in the marsh as a whole (Mihelsons, 1981).

The recruitment rate of autochtonous one-year-old females (Rt2) and one-year and two-year-old females (after two years) together (Rt 2+3) gives in most cases the best correlation with the density indices for the whole marsh (Table 3). The difference from random recovery rate may be due to various causes and further investigations are needed. We suggest that Re2 and Rt2 (or Rt 2+3) characterize the post-hatching survival in various periods. Re2

Table 2. Correlation between the indices of density[a] and relative survival rate (Re2)[b] of juvenile Tufted Ducks in 6 limited areas (A-F) of Engure Marsh, Latvia, 1967, 1969-1976

| Re2 in area | Index of density in area | | | | | | |
|---|---|---|---|---|---|---|---|
| | A | B | C | D | E | F | Total area |
| A | −0.48[c] | −0.03 | −0.40 | +0.22 | +0.51 | −0.06 | +0.25 |
| B | −0.30 | −0.79* | −0.62 | −0.57 | −0.12 | −0.43 | −0.44 |
| C | +0.04 | −0.63 | −0.67 | −0.42 | +0.09 | −0.44 | −0.27 |
| D | +0.08 | −0.31 | −0.23 | −0.67 | −0.45 | −0.58 | −0.44 |
| E | −0.11 | −0.10 | −0.12 | −0.51 | −0.58 | −0.54 | −0.50 |
| F | −0.13 | −0.16 | −0.23 | −0.38 | −0.10 | −0.44 | −0.08 |
| Total area | −0.06 | −0.46 | −0.50 | −0.49 | −0.16 | −0.54 | −0.37 |

[a] Total number of nests in the given year expressed as a percentage of the 3-year moving average;
[b] Random recovery rate during second calendar year of life;
[c] The highest negative value of correlation coefficient in each row is encircled;
* = $p < 0.05$.

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Table 3. Correlations between the indices of density[a] and the recruitment rate to first breeding of autochtonous one-year and two-years-old (Rt 2+3) female Tufted Ducks in 6 limited areas (A-F) of Engure Marsh, Latvia, 1967, 1969-76

| Rt 2+3 in area | Index of density in area | | | | | | |
|---|---|---|---|---|---|---|---|
| | A | B | C | D | E | F | Total area |
| A | −0.52 | −0.22 | −0.60 | −0.27 | −0.32 | −0.63[b] | −0.62[b] |
| B | −0.09 | −0.63 | −0.04 | −0.60 | −0.26 | −0.57 | −0.55 |
| C | −0.24 | −0.36 | −0.57 | −0.49 | −0.35 | −0.68 | −0.62 |
| D | −0.43 | −0.26 | −0.54 | −0.09 | −0.20 | −0.38 | −0.49 |
| E | −0.50 | −0.12 | −0.44 | −0.04 | −0.39 | −0.36 | −0.62 |
| F | −0.46 | −0.27 | −0.61 | −0.28 | −0.28 | −0.61 | −0.59 |
| Total area | −0.46 | −0.22 | −0.55 | −0.28 | −0.40 | −0.59 | −0.67* |

[a] As in Table 2;
[b] The two highest values of correlation coefficients in each row are encircled;
* = $p < 0.05$.

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shows the relative survival rate of young ducks during first months of post-hatching period (i.e. mainly till the end of first calendar year of life), Rt2 embraces more prolonged period (mainly during almost all first year of life till the first breeding). Data from the literature on other species suggest that more or less intense regulation of numbers may continue also during

T a b l e  4. Correlations between the index of the absolute number of
survived juvenile[a] Tufted Ducks and the recruitment rate (Rt2) of autochto-
nous one-year-old females in 3 areas[b] with different survival of juveniles,
Engure Marsh, Latvia, 1967, 1969-76

| Rt2 in area | Index of the absolute number of survived juveniles in area | | |
|---|---|---|---|
| | A | D | G |
| A | −0.53 | −0.05 | +0.68[*] |
| D | −0.62 | −0.33 | +0.78[*] |
| G | −0.77[*] | −0.28 | +0.49 |

[a] See text for explanation;
[b] Areas with different survival of juveniles: A − high, D − medium,
G − low;
[*] = $p < 0.05$.

migration and in winter quarters, for example, due to competition for better
feeding places within the population. In such cases it should be more reflec-
ted in the Rt2 than in Re2 and a relationship should exist between competiti-
ve ability and survival.

As we do not know the competitive ability of juveniles we compared the
survival of ducklings of three female groups which differ in their mean com-
petitive ability (or social rank) in choosing their nest sites: 1) the hig-
hest (A) − from island A with the highest mean survival of offspring; 2) me-
dium (D) − from 4 small islands, and 3) the lowest (G) − from slough area
of the marsh where the survival of ducklings usually is the lowest. Instead
of the unknown absolute number of juveniles surviving till their migration
from the marsh, relative indices were used in the calculations. The indices
were obtained by correcting the number of recoveries during the period bet-
ween the first exodus from the marsh till the end of the second calendar
year to allow for 100% ringing. Correlation coefficients were calculated bet-
ween the obtained data on juveniles of each category and the corresponding
Rt2. The results turned out to be convincing (Table 4). With the increase of
the absolute number of migrating offspring produced by females of the highest
social rank (A), the next spring Rt2 in all three categories decreases and
the highest decrease of the return rate was for females from the lowest  so-
cial rank (G). The number of surviving juveniles from the medium rank has a
smaller negative effect but from the lowest rank even significant positive
correlation was observed. The latter phenomenon is not yet understood. Besides
there are other indications confirming that ducklings produced by females of
the highest rank are really more capable of competition than those produced
by females of the lowest rank. In the Tufted Duck and especially in the Shove-
ler the juveniles of one-year-old females in years of high population density
were significantly more often recovered outside the natal marsh than juveni-
les of the same age in years of low population density (Mihelsons, Mednis,

1976). Evidently if competition is higher the juveniles have to leave the En-
gure Marsh earlier.

In summary, the given facts on the Tufted Duck prove indirectly that popu-
lation self-regulation is a prolonged step-by-step process with various dyna-
mic stages, in which migrational homing of adult females and their ability for
competition, i.e., hierarchial rank in the population, are especially important.

R e f e r e n c e s

Anderson D.R., Burnham K.P. Population ecology of the Mallard. VI. The ef-
    fect of exploitation on survival. U.S. Dept. Int. Fish Wildl. Serv.
    Resour. Publ., 1976, 128.
Blums P.N., Reders V.K., Mednis A.A., Baumanis J.A. - J. Wildl. Manage,
    1983, 47 (1).
Boag D.A., McCourt K.H., Herzog P.W., Alway J.H. - Can. J. Zool., 1979, 57,
    p. 2275-2284.
Dhondt A.A. - In: Proc. Adv. Study Inst. Dynamics Numbers Popul. (Oosterbeek
    1970), 1971, p. 532-547.
Kluyver H.N. - In: Proc. Adv. Study Inst. Dynamics Numbers Popul. (Oosterbeek
    1970), 1971, p. 507-523.
Lejins G. - The Ring, 1964, 41, p. 75-76.
Mednis A.A., Blums P.N. - In: Ringing in the study of bird migration in fauna
    of the USSR / Ed. by V.D.Ilyichev. Moscow, 1979, p. 157-167
Mihelsons H.A. - In: Proc. Int. conference on conservation of wetlands and
    waterfowl, Heiligenhafen 1974. 1976, p. 394-400.
Mihelsons H.A. - Acta Orn., 1980, 17, p. 45-62.

Mihelsons H.A. - In: X Baltic Ornith. Conf. Riga 1981. 1981, p. 120-125
    (in Russian).
Mihelsons H.A., Blums P.N. - Lintumies, 1976, 11, p. 98-106
Mihelsons H., Lejins G., Mednis A. - In: VII Baltic Ornith. Conf. 3, Riga
    1970. 1970, p. 43-47
Mihelsons H., Mednis A. - In: IX Baltic. Ornith. Conf. Vilnius 1976.
    1976, p. 164-168
Mihelsons H., Mednis A., Blums P. - In: Proc. Int. Symposium on the mapping
    of waterfowl distributions, migrations and habitats, Alushta 1976.
    1981a, p. 293-311.
Mihelsons H., Mednis A., Kastepold T., Kastepold E. - In: Proc. Int. sympo-
    sium on the mapping of waterfowl distributions, migrations and habitats,
    Alushta 1976. 1981b, p. 312-321.
Mihelsons H.A., Mednis A.A., Kastepold E., Kastepold T. - In: X Baltic
    Ornithol. Conf. Riga 1981, 1981c, p. 126-130
Zwickel F.C. - Can. J. Zool., 1980, 58, p. 896-905.

# COMPLEX VISUAL INFORMATION PROCESSING IN THE PIGEON

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## INTRODUCTION

In the normal environment of an animal one and the same object can yield very different patterns of retinal activation depending on the particular lighting conditions and on the relative orientation and distance the object has with respect to the animal's eyes. It is nevertheless imperative for the sake of evolutionary fitness that animals positively recognize at least a range of objects in spite of this apparent variability. Furthermore it is equally important that different objects be recognized by some abstract criteria as belonging to one of several classes of objects. To these classes the animal can then respond with relatively unitary sets of responses in spite of the individual diversity of the member objects. We humans of course make constant use of such capabilities in the course of daily life with respect to scores of objects. Psychologists give the collective names of perceptual invariance and perceptual concepts to the phenomena underlying these competences. Engineers have recently made efforts to provide robots with comparable performances. While their implementation is feasible in principle it has been found that they require an inordinate amount of computing power. Small-brained animals such as birds are necessarily short of information processing capacity and may thus have to forgo some perceptual invariance and concept capabilities. But the impression of field students of avian behaviour is that, if anything, the visual performance of most birds outclasses their own. For some basic functions this impression has indeed been supported by formal research. Pigeons (Columba livia) for example have colour vision that is more sophisticated than ours in being at least tetrachromatic with a spectral sensitivity extending into the near-ultraviolet and an additional abilty to detect the polarization plane of light (Emmerton, Delius,1980; Delius et al., 1976).

## ROTATION INVARIANCE

We have recently begun to examine experimentally the extent of pigeons' visual invariance abilities. With Valerie Hollard (Auckland, New Zealand) we studied their performance in a situation that demands the visual identification of specific forms when these appear at various angular orientations. This requires a mechanism that ensures a rotational invariance of pattern recognition. More specifically, the birds had to repeatedly recognize a predetermined target out of pairs of mirror-image shapes when these were displayed at angular orientations coinciding or not coinciding with the target's alignment. To get the pigeons to perform the task we employed an operant discrimination learning paradigm known as matching-to-sample (Carter, Werner, 1978). The food-deprived birds were placed in a three-key Skinner-box. An automatic slide projector displayed shapes on the back of the translucent keys. The opening of a shutter first allowed the pigeons to view the target or sample shape projected on the middle key. The birds were required to acknowledge this stimulus by pecking the key a number of times. This caused the two side-key shutters to open, exposing the two comparison patterns on them. One of these

804

patterns wae geometrically identical to the sample pattern. The other pattern was its mirror image. The pigeons of one group had then to peck the key wearing the identical, matching, those of another group of birds, the odd, non-matching ehape. If they did so correctly they were rewarded with brief access to food, if they chose the wrong shape they were punished with a brief period of darkness. The next trial began with the presentation of the next sample and so forth. The daily sessions consisted of 40 such trials. After training for some 40 sessions with sets where the orientation of sample and comparison stimuli were the same, series of 10 seseione wsre conducted with sets of stimuli that systematically explored the effect of angular disparities between samples and comparison shapes. The order in which the various stimulus eete occurred was randomized, as was of course the sequence in which the correct and incorrect stimuli appeared on the left and the right response keys. The whole procedure was controlled by a suitably programmed microcomputer which aleo recorded all the pertinent data, in particular the correct or incorrect nature of the reeponse in each trial as well the latency or reaction time corresponding to each response. This is the time interval between the oneet of the comparison stimuli and the peck to one of them for each trial (Hollard, Delius, 1982).

It was found that pigeons could master the task quite efficiently. Error rates could be as low ae 10% and the reaction times as fast as 0.7 sec. The most important result however was that the error rates and the reaction times were nearly constant, that is neither varied significantly as a function of the degree of orientation disparity between the samples and the comparison patterns. In other words the pigeons found it equally easy to identify the matching (or non-matching) comparison patterns, regardless of whether these were oriented the same way as the sample (0 degreee) or tilted by 45, 90, 135 or even 180 degrees clockwise. This was so irrelevantly of whether the pigeons were dealing with patterne and their mirror images with which they had had extensive previous experience or with totally new patterns. Essentially the same results were aleo obtained if the oomparison stimuli were always shown in the standard orientation but the samples were presentsd in varying angular positions between 0 and 180 degrees (Fig. 1).

This result is remarkable becsuse previous experiments (Cooper, Sheppard, 1978) as well as our own using students inetead of pigeons (Hollard, Delius, 1982), have shown that the performance of humans in this kind of task is markedly dependent on the degree of rotation of the comparison patterns. Particularly the reaction times are a monotonically incrsasing function of the disparity angle. Overall, humans were also much slower in responding than the pigeons. The interpretation supported by introspective accounts is that humans have to rotate a memory representation of the sample stepwise, each time comparing it for coincidence with the comparison stimuli. This sequential procedure, known as mental rotation, has all the characteristics of thinking or, as psychologists prefer to say nowadays, of a cognitive process. Pigeons obviously solve the problem in a different, more immediate, automatic way that in earlier times might have been labelled as reflexive or even instinctive. Parallel rather than sequential information processing seems to be brought into play by their visual system.
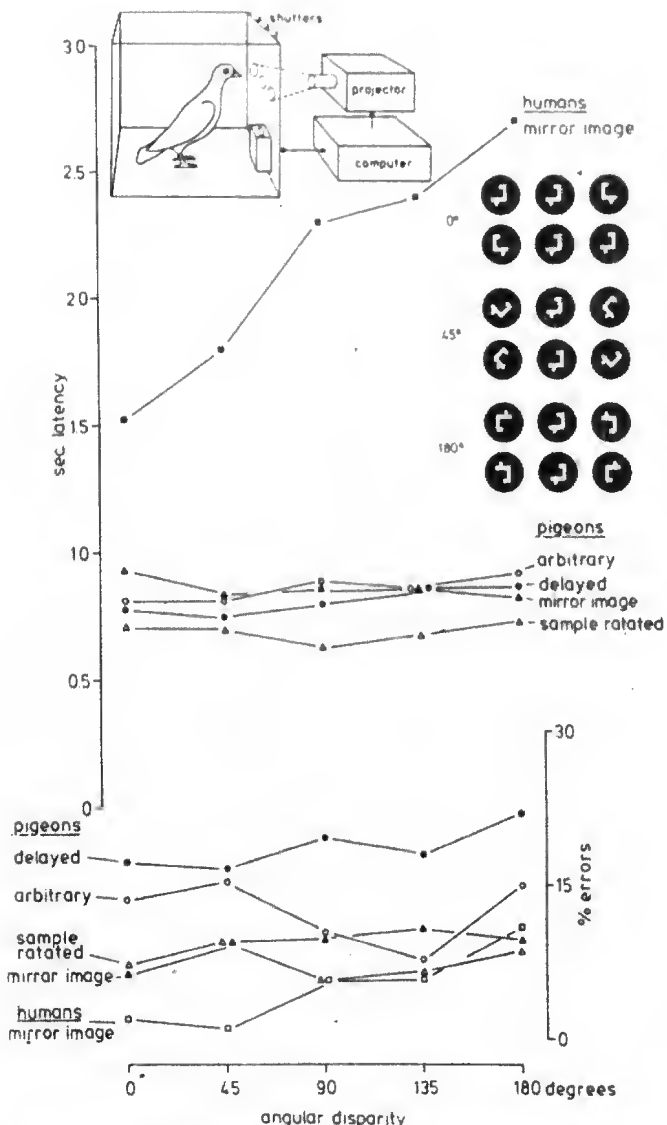
F i g. 1. Latencies and error rates of pigeons and humans during rotational invariance tasks with visual patterns. The insets illustrate the apparatus employed and give examples of the matching-to-sample tasks (see text for further details)

Most of the studies on mental rotation in humans, although not ours, were done with a procedure that required the subjects to refer to the sample or target as an engram, that is as information stored in memory. We considered that perhaps this might be an important factor. Experiments with pigeons in which the sample pattern was shut off 5 sec before the comparison stimuli came on, a delayed matching-to-sample procedure, led to some deterioration of performance but there was still no evidence of any dependence on the orientation disparity of the forms (Fig. 1).

Now, humans yield a performance similar to that of our pigeons in an other kind of rotational invariance task where instead of mirror images the

odd patterns are arbitrarily different shapes (White, 1980). Just in case, we have tested pigeons with an analogous task and found that their performance was the same as when they dealt with mirror-image pairs of shapes. There is considerable evidence that for humans mirror-image shapes are peculiarly difficult to distinguish (Corballis, Beals, 1976). It seems possible that for pigeons this is not so and preliminary experiments of ours suggest that they may indeed find them easy to discriminate.

This suggests that the sequential, mental rotation process might only be brought into play when the shapes to be distinguished are very difficult to discriminate. For humans there is an indication that indeed mental rotation results are obtained with non-mirror-image odd shapes only when the shapes are highly complex. Perhaps pigeons would also yield such a performance if one would select shapes that are especially hard for them to discriminate. Visual pattern discriminations as compared with colour and brightness discriminations are more difficult for pigeons than they are for humans, thus the experiment involving non-mirror images might have already fulfilled this condition but this issue needs further experimentation. Alternatively one can hypothesize that pigeons store information about shapes in an orientation-free mode. They thus should have difficulty with tasks demanding the discrimination of one and the same shape at different orientations. We have found that pigeons indeed have considerable difficulty in learning to discriminate an upright cross + from a tilted cross x (Delius, Emmerton, 1978). This could have to do with the fact that pigeons operate visually predominantly on the horizontal plane where the orientation of objects is largely arbitrary relative to the position of the observer. Humans view predominantly the vertical plane where both observer and objects tend to have an orientation determined by the effects of gravity. Pigeons have however been shown capable of discriminating very small angular orientations disparities of line stimuli (Klipec et al., 1979) and thus this explanation can be only a partial one.

We have further wondered whether the rotational invariance performance of pigeons might be due to the fact that they have a visual system predominantly based on the midbrain optic tectum as compared with the mammals that have a mainly endbrain, striate cortex based system. As a first step we examined the performance of our pigeons after they had been surgically deprived of their telencephalic Wulst, a brain area that contains the avian homologue of the mammalian visual cortex. Their invariance performance was completely unaffected. Thus the information processing required for it clearly does not take place there. This contrasts with the consequences of visual cortex ablations in primates who are then very nearly blind and certainly incapable of mental rotation (Milner, 1970).

VISUAL CONCEPTS

In the research summarized above we made the assumption that pigeons are capable of detecting the identity or conversely the oddity of sample and comparison shapes in a generalized, concept-like fashion. However there has been controversy as to whether pigeons really can achieve this (Carter, Werner, 1978). Since our pigeons' matching-to-sample performance in the rotational invariance tests was maintained even when they had to deal with shapes completely new to them (Hollard, Delius, 1982) we have no doubt that they can. If

previous experimenters had some difficulty with demonstrating a conceptualization of identity/oddity by pigeons then we believe that this has been due to the employment of too few training stimuli, inviting the pigeons to use simpler strategies, and to the use of designs that allowed the strong novelty aversion that characterizes these animals to come into play.

There is another way in which the issue of whether pigeons can conceptualize is relevant here. We mentioned earlier that it is possible that pigeons in contrast to humans distinguish between mirror-images shapes just as well as between any arbitrarily different shapes. This suggests that the birds may not be able to recognize the special equivalence of mirror-image shapes. That could imply that pigeons may not recognize bilaterally symmetric shapes as a particular class of forms consisting of two fused mirror-image halves. Morgan et al. (1976) have mentioned evidence that supported this view but Delius and Habers (1978) found that pigeons seemed to be able to discriminate bilaterally symmetric from asymmetric shapes in a generalizing manner.

With Brigitte Nowak we have investigated this issue more thoroughly. Pigeons were trained to discriminate 26 bilaterally symmetric shapes from an equal number of asymmetric shapes using a free operant successive discrimination procedure (Delius, Nowak, 1983). The shapes were back-projected onto the single key of a Skinner-box in a randomized sequence. Each shape was shown for a standard 30 sec. One group of pigeons was required to peck the symmetric pattern for occasional food reward and not to peck the alternative patterns to avoid extensions of the presentation time of the non-rewarded stimulus. Performance was measured by the percentage of responses to the correct stimuli out of all responses during the standard 30 sec presentations. The daily sessions involved the displaying of 40 shapes. All pigeons learned to perform at a level of 80% or more responses correct within 25 sessions. In interspersed trials they were then exposed to test shapes with which they had no previous experience with under extinction conditions, that is where responses had no consequences. The birds classified these stimuli with high accuracy, that is they responded with high frequency to the novel stimuli that belonged to the same class as those training stimuli that had yielded reward and much less to those that were of the same type as those training stimuli that had resulted in punishment. This was so even when the geometrical style of the test figures differed markedly from the training shapes (Fig. 2).

There can be no doubt that the pigeons recognized the bilateral symmetry, or else the asymmetry, of the figures in a concept-like, generalized fashion. They did so regardless of the fact that in one test series the asymmetric stimuli were repeated shapes especially designed to have a redundancy at l least as high as that characterizing symmetric forms and that in another series the test figures were presented with varied symmetry axis orientations, differently from the training stimuli which always had a vertical axis. The pigeons' symmetry recognition was not impaired when they had to perform with one eye covered by an eye-patch. The competence for symmetry recognition can not thus be somehow ascribed to the bilateral symmetry of the nervous system. The mechanisms with which pigeons recognize symmetry do not seem to correspond pond with any that have been proposed to explain symmetry identification by humans (Corballis, Beale, 1976). Rather we have put forward an alternative theory of our own.
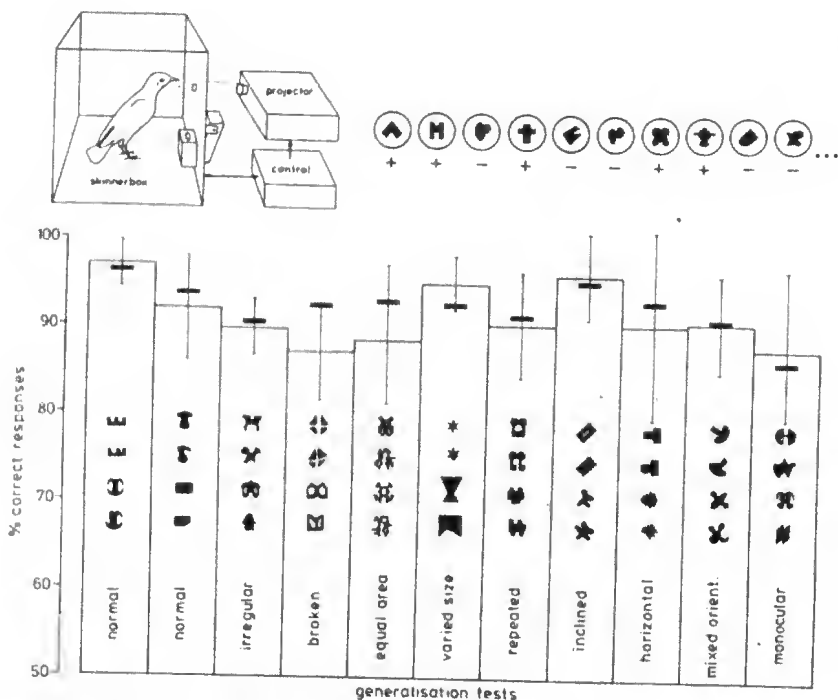
F i g. 2. Mean correct response scores (cloumns) of pigeons generalizing a symmetry/asymmetry discrimination to various sets of novel visual patterns (examples shown). The concurrent performance on the training stimuli is indicated by bars. The insets illustrates the apparatus employed and the successive discrimination conditioning with examples of the training stimuli

It is known that the visual system of both birds and mammals performs a kind of spatial Fourier analysis (De Valois, De Valois, 1980; Jassik-Gerschenfeld, Hardy, 1981). If symmetric and asymmetric shapes are examined from this point of view one finds that at the symmetry axis the Fourier components have a special phase relationship being all in-phase (0 degrees) and/or anti-phase (180 degrees) to each other whereas such conjunction does not occur anywhere in an asymmetric pattern. There is evidence that these phase relationships have a special status for humans (Atkinson, Campbell, 1974) and there are reasons to expect that the same is true in birds. This has to do with the fact that both visual systems have to deal with an information surface, the retinal image. This can only be done with neuronal networks that have a multiply symmetrical microstructure.

If such neural filters are the basis of symmetry recognition it seems unlikely that our pigeons developed them during training. Rather it must be suspected that they only learned to apply pre-existing ones to the task in hand. Additional experiments suggest that naive adult pigeons have a slight but consistent spontaneous preference for asymmetric patterns and that they can bring a symmetry/asymmetry recognition to bear at a very early stage of discrimination learning. We assume, admittedly so far without proof, that, as it is apparently the case in humans (Bornstein et al., 1981), the relevant networks are laid down very early in neurogenesis and predominantly

under genetic control. If that is so one may doubt whether it is appropriate
to talk about a symmetry concept. That is a matter of definition but pigeons
have of course been shown able to truly learn a variety of other perceptual
concepts such as people, person, tree, oak leaf, pigeon, fish, and so forth
(Herrenstein, de Villiers, 1980).

Returning to symmetry recognition one may ask about its adaptive value.
Refering to insectivorous birds Curio (1976) suggested that it may aid them
to break the camouflage of some of their prey. For pigeons and as a matter
of fact humans it is more difficult to make such a case. Rather, as already
indicated above, we believe that visual symmetry is really a by-product of
structures selected to fulfil other more general visual information proces-
sing functions.

CONCLUSION

In spite of their relative microcephaly, implying limitations in informat-
ion processing capacities pigeons and presumably other birds perform at least
some perceptual invariance and conceptualization functions which are known to
be highly demanding on computing power. In at least one instance the pigeon's
performance was found to be superior to that of the macrocephalic human
species.

ACKNOWLEDGEMENTS

R e f e r e n c e s

Atkinson J., Campbell F.W. - Vision Res., 1974, 14, p. 159-162.
Bornstein M.H., Ferdinandsen K., Gross C.G. - Develop. Psychol., 1981, 17,
    p. 82-86.
Carter D.E., Werner T.J. - J. exper. Anal. Behav., 1978, 29, p. 565-601.
Cooper L.A., Shepard R.N. - In: Visual Information Processing / Ed. by
    W.G.Chase. N.Y.: Academic Press, 1973.
Corballis M.C., Beale I.L. The Psychology of Left and Right. Erlebaum, Hills-
    dale, 1976.
Curio E. The ethology of predation. B.; N.Y.: Springer, 1976.
Delius J.D., Perchard R.J., Emmerton J. - J. Comp. Physiol. Psychol., 1976,
    90, p. 560-571.
Delius J.D., Emmerton J. - In: Animal Migration, Navigation and Homing / Eds.
    K.Schmidt-Koenig, W.T.Keeton. B.; N.Y.: Springer, 1978.
Delius J.D., Habers G. - Biol., 1978, 22, p. 336-342.
De Valois R., De Valois K.K. - Ann. Rev.Psychol., 1980, 31, p. 309-341.
Emmerton J., Delius J.D. - J. Comp. Physiol., 1980, 141, p. 47-52.
Herrnstein R.J.,Villiers P.A. de. - Psychol. Learn. Motiv., 1980, 14, p.59-95.
Jassik-Gerschenfeld D., Hardy O. - Vision Res., 1981, 21, p. 745-747.
Klipec W.D., Lindblom L., Lindblom L. - Anim. Learn. Behav., 1979, 7, p.75-79.
Milner P.M. Psychological Psychology. L.; N.Y.: Holt, Rinehardt and Winston,
    1970.
Morgan M.J., Fitch M.D., Holman J.G. - Lea S.E.G. Perception, 1976, 5, p.57-66.
White M.J. - Bull. Psychon. Soc., 1980, 15, p. 153-156.

# THE EVOLUTION OF HIGHER LEARNING ABILITIES IN BIRDS

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## INTRODUCTION

Ornithologists at one time felt that the intellectual capacities of birds were rather limited. Several factors combinet do produce this opinion. Birds lack the cerebral cortex so predominant in mammals. Some ornithologists suggested that the ability to fly allowed birds to remain stupid, "Flight has proven to be an enormously successful evolutionary venture, but one that has cost birds dearly in mental development. In effect, flight has become a substitute for cleverness; birds solve many potential problems merely by flying away from them... As a consequence, much (avian) behavior is, by mammalian standards, fragmentary, stereotyped, and at times amazingly stupid." (Welty, 1962, p. 159).

We now know that this view must be altered. The avian hyperstriatum provides a neurophysiological substrate for learning in birds (Stettner, Matyniak, 1968). Research in behavioral ecology on situations such as foraging for patchily distributed food or mate selection has made it clear that being able to fly leaves many problems unresolved (Krebs, Davies, 1978). Most critically, evidence on learning in birds which has been collected recently makes it quite clear that many birds are not stupid at all; indeed, some birds possess quite sophisticated cognitive abilities.

Much of this evidence has come from psychological research on learning. Biologists and psychologists have studied learning in distinctly different ways. Biologists have concentrated upon specific types of learning such as imprinting and song learning. I call these specific because they involve specific responses to particular stimuli, and appear to serve specific biological functions, such as species recognition or attracting a mate. Psychologists,on the other hand, have tended to study more abstract types of learning, attempting to uncover and delineate a few types of learning which might be general across species and across situations. Some of these types of learning involve quite complex situations, requiring the animal to abstract much information from the environment and act in what is, essentially, a cognitive, intelligent manner. While this psychological research suffers from the disadvantages of arbitrary, often highly contrived laboratory situations, it has the advantage of making the cognitive abilities of birds particularly clear in terms which allow comparisons with other groups of animals.

I have three major goals in this paper: (1) To present some of the results of our research on learning in birds which demonstrates quite sophisticated problem solving abilities; (2) To discuss some interesting evolutionary questions raised by these results; and (3) To suggest some important contributions ornithologists can make to resolving these issues.

The high levels of learning abilities posseseed by at least some birds is revealed by their capacity for learning set formation. In a learning eet experiment, the animal is presented with many different problems of the same type. If the animal learns to solve new problems more quickly as a function of its previous experience with other, similar problems, then learning set has been acquired. This is sometimes called learning to learn (Harlow, 1949).

The type of learning set most frequently studied is known as object diecrimination learning set. In this type of learning set, each individual problem consists of an object discrimination problem in which the animal chooses between two different objects. One of thsse objects is arbitrarily designated correct and covers food. The animal makes ite choice by displacing one of the objects. If the correct object is displaced, then the food is found. If the incorrect object is displaced, no food ie found. During each problem the animal is allowed to make several choices between the two objects, each choice constituting a trial. Then a new problem is begun by introducing a new pair of objects. The most sensitive measure of learning set is the percentage correct choices on the second trial (Trial 2) of new problems. Since each problem involves a new pair of objects, with the correct object designated arbitrarily by the experimenter, it is impossible for the animal to be correct more than half the time on Trial 1. However, once the animal hae acquired the information offered by the outcome of the first trial, perfect performance is theoretically possible on Trial 2. Suppose one of the objects is red and the other blue, and that the animal chose the red object on Trial 1. If the choice of the red object uncovered food, then it is the correct object. If choice of the red object did not produce food, then the blue object must be correct.

The acquisition of a learning set is a eophisticated feat, since it requiree the abetraction of a general principle which can be applied to new problems. Comparative research on object discrimination learning set has shown that there is a lot of variation in learning set ability among mammals.Figure 1 is taken from a review of this literature by Warren (1965), and shows the Trial 2 performance of eeveral mammalian species. The pattern of results appear to correlate with some sort of phylogenetic "scale", with primates performing best.

At this time, in the mid-1960s, the literature suggested that non-mammalian species, including birds, could not acquire a learning set. However, the only avian research bearing on this issue had been carried out using pigeone (Columba livia) as subjects (Zeigler, 1961), and it seemed likely that work with other species might yield very different results. This prompted me to begin a research program into avian learning set ability with several species, particularly the Blue Jay (Cyanocitta cristata). We used procedures almost identical to those that had been developed for use with primates. In most primate research, thres-dimeneional objects are used, which vary in color, brightness, size, shape, etc., and the animals move these objects with their hands. We use the same technique, except that the birds displace the objects with their beaks. As in the primate research, the jays were given a series of several hundred problems, each defined by a new pair of objecte, and each con-
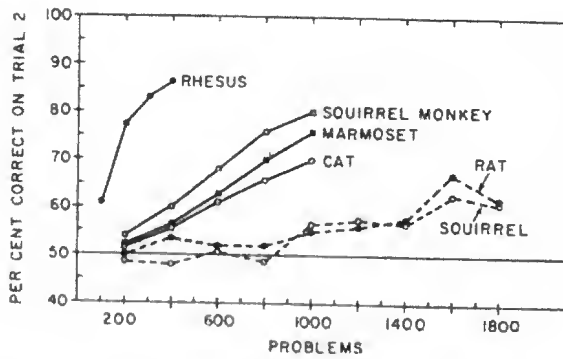
F i g. 1. The performance of Trial 2 of new problems during learning set experiments by several mammalian species (from Warren, 1965)

sisting of several trials. The learning measure we emphasized was percentage correct on Trial 2 of new problems, the first trial on which performance can exceed chance levels.

Blue Jays perform very well in such learning set experiments. For example, in our first experiment (Hunter, Kamil, 1971) with Blue Jays, performance on Trial 2 increased rapidly, and approached asymptotic levels of approximately 75% correct. This level of performance is equal or superior to that of many mammals, even some primates. At least some avian species, and we have similar data for Myna Birds (Gracula religiosa, Kamil and Hunter, 1969), are capable of very good learning set acquisition.

The similarity between Blue Jays and primates is dramatic. But do the Blue Jays actually achieve this learning through cognitive processes similar to those of primates? Much of the primate research on learning set has been directed towards discovering how the animals go about solving new problems so rapidly. The evidence indicates that Rhesus monkeys and chimpanzees do well on learning set because they manage to extract a strategy or rule from the procedure that is best labeled a win-stay, lose-shift strategy. It simply requires the animal to recall what happened on the previous trial and respond accordingly. If the animal won (received food), it should stay with the same object that it did not receive on the previous trial, then it should shift away from the stimulus it had chosen on the previous trial, lose-shift. Thus the label win-stay, lose-shift is descriptive (Bessemer, Stollnitz, 1971).

Is the learning set ability of Blue Jays due to the same strategy learning? We began a program of research in my laboratory to determine if the win-stay, lose-shift strategy was in fact used by Blue Jays. To make a long story short, we replicated all of the critical experiments from the primate literature in detail. We found that the behavior of the Blue Jays was similar to that of the primates in demonstrating the use of a win-stay, lose-shift strategy in all respects.

Let me describe two of these results. One implication of the win-stray, lose-shift strategy is that there are two kinds of information that the learn-

ing set experienced animal possesses. One ie that strategy itself, which the animal hae learned and should not forget, at least not rapidly. And indeed, in both Blue Jays and monkeys, the ability to solve new problems is undiminished by long periods in which the animal is not tested, as long as 6 months or a year or more (Kamil, Lougee and Shulman, 1973).

On the other hand, the ability to perform well on the current problem should be much less stable since it preeumably depends upon the contents of a relatively dynamic memory of the events of the previous trial. Thie can be tested by inserting a retention interval in the midst of a problem. That is, give the bird or the monkey several trials on a single problem then make him wait two minutes, four minutes, eight minutes, 24 hours, and then give him another trial. If performance declines as a function of this retention interval, then the dynamic, short-term memory exists. The next slide showe that when you do this with Blue Jays quite rapid memory loss for particular problems occurs. These results are almost exactly similar to those obtained with Rhseue monkeys (Kamil, Lougee and Shulman, 1973).

An even more impreseive demonetration of similarity between Blue Jays and monkeys can be found in the phenomenon known as reversal training tranefer to learning set. Reversal training consists of taking just two stimuli, for example a black object and a white object, and arbitrarily designating one of them correct, say the black object. The animal is allowed to choose between the two objects repeatedly. Once it has learned that the black object is correct, the reward values of the two objects are reversed so that the white object becomes correct. This training now continues until the animal learns that the white object is correct. Then another reversal takee place and the black object becomee correct. This continues for many reversals.

Several different rules could be ueed by an animal to successfully solve reversal training. One of these is the win-stay, lose-shift rule. Suppose the animal simply stays with a particular object as long as it is rewerded, and then shifts its behavior to the other object when not rewardsd. The result would be just one error per reversal. If animals use win-stay, lose-shift rules during both reversal training and learning set one would expect a high degree of transfer. That is, if animals were trained first on reversal learning and then ehifted to learning set, they should perform well on learning set. This occurs in chimpanzees and Rhesus monkeys, but does not occur in other mammals such as squirrel monkeys or cats (Schusterman, 1962; Ricciardi, Treichler, 1970; Warren, 1966). When we performed this experiment with Blue Jays (Kamil, Jones, Pietrewicz, Mauldin, 1977), we found a high degree of transfer from reversal learning to learning set. This provides unambiguous evidence for the ability of the Blue Jay to abstract the win-stay, lose-shift rule from experience with a single pair of objects during reversal training, an ability apparently not posssssed by cate (Warren, 1966) or squirrel monkeys (Ricciardi, Treichler, 1970).

Theee reeults demonstrate high levels of at leaat one cognitive ability do exist in birds. Other experimenters are also finding such results in other tasks (Balda, 1980; Kruchinsky, Zorina, Dashevsky, 1979; Pepperberg, 1981; Vander Wall, 1982). The traditional view of birds as relatively stupid animals must be abandoned.

The learning set literature also demonstrates that there is considerable variation in cognitive ability amongst both mammals and birds. Figure 1 showed some of the mammalian variation. An experiment by Mauldin and Kamil demonstrates the variation that exists among birds. We tested pigeons for learning set acquisition exactly as we have tested Blue Jays. The pigeons were quite willing to behave in this apparatus, and they were able to learn individual problems. However, they showed no indications of learning set. They continued to solve problems at the same slow rate, even after several hundred previous problems, and their performance on Trial 2 never rose above chance levels. This result with pigeons shows that the acquisition of learning set is not, strictly speaking, an artifact of the procedures used. If the procedures forced the learning set result, then pigeons would show learning set.

Finally, these results demonstrate a remarkable similarity between the cognitive abilities of some birds and some mammals. Such similarities in intellectual ability between quite different species may become a common theme in the 1980's. For example, Couvillon and Bitterman (1980) have recently found that many of the basic phenomenon of Pavlovian conditioning are virtually identical in honeybees and mammals. The variations and similarities in cognitive abilities among and between different groups of animals raises some very interesting evolutionary issues. If we think of man as an unusually cognitive animal capable of general learning then we should attempt to understand how such learning abilities might have evolved. One of the difficulties we will face in this endeavor is making the connection between the learning problems that we use in the laboratory and the natural life of the animal. If these cognitive abilities evolved because they have adaptive significance for the animals that possess them, we must understand their adaptive significance to understand their evolution.


ADAPTATION AND LEARNING

Although the existence of such a connection between abstract learning abilities and adaptive significance may appear unlikely, it seems to me there can be little doubt that connections exist. For example, consider the research that Larry Wolf and Reed Hainsworth of Syracuse University and I have conducted on spatial learning in hummingbirds. One of the things we know about the natural ecology of the hummingbird is that when it visits a flower it tends to empty that flower of nectar. Therefore, if the animal can remember which flowers it has visited, it should tend to avoid revisits to those flowers, a kind of win-shift strategy. This suggests that the animal should be able to learn to shift away from the previous site of reward more easily than to learn to go back to the same site.

Therefore, we set up an experiment using artificial flowers in the laboratory in which the animal was required to either stay or shift. The basic design of the experiments was quite simple. First, on each trial the animal was given one flower to feed from and it emptied that flower. Second, two flowers were presented and the hummingbird was given a choice between going back to

that same location or going to another location. If the bird was in the stay condition, then it had to remember where it had just been and go back; win-stay. If it was in the shift condition, it had to remember where it had just been and go to the other location; win-shift. Eight hummingbirds were tested under both the stay and the shift conditions. The results were quite dramatic. Regardless of whether the stay learning came first or second, stay learning always took much longer than shift learning, in some cases as much as 5 to 6 times as long. The stay learning generally took place very slowly while shift learning took place very rapidly (Cole, Hainsworth, Kamil, Mercier and Wolf, in press). This demonstrates a clear connection between the natural ecology of the animal and its performance in a cognitive task. This type of result suggests that at least some of the variation in cognitive abilities may be capable of being understood in terms of adaptations to specific environments.

However, we must also deal with the question of marked similarity between very different species. There are several possibilities we must investigate. One is that these general types of learning, these cognitive abilities, are not really general at all. That is, they may be tied to the specific adaptations of specific animals. In that case we must apply a comparative ecological approach and compare and contrast closely related animals of different ecologies and distantly related animals of similar ecologies.

Another possibility is that certain kinds of learning seem to be quite general in very disparate species because there are some very general aspects of the environment and/or the nervous system which creates this generality. In terms of the environment, it may be that the environments of many animals are so constructed that certain kinds of learning abilities will always be of adaptive advantage. In terms of physiology, it is possible that some very basic characteristics of the nervous system, such as the fact that neurons always fire in all-or-none fashion, place constraints upon the kinds of learning processes animals may possess.

In any event, ornithologists can make important contributions to the resolution of these issues. Historically, the study of complex learning has been carried out mostly in mammals. If we are to begin to test evolutionary questions about the appearance of learning, then much work needs to be done with birds. For example, if the mammalian literature suggests that certain types of learning abilities are characteristic of generalists as opposed to specialists, this hypothesis could be tested in a separate group of animals and the birds are a perfect group for such tests. Furthermore, because there are so many avian species, and they vary so much in their adaptations, many hypotheses might be generated by original research of cognitive abilities in birds. Thus I believe that research with birds could be of critical importance in developing an understanding of the adaptive significance and evolution of the cognitive abilities of animals.

### SUMMARY

Blue Jays (Cyanocitta cristata) perform better than some mammals, and as well as some primates, on learning sets, a higher order learning task. The Blue Jays acquire learning sets in a manner virtually identical to that used

by Rhesus monkeys and chimpanzees, by abstracting a general strategy which can be applied to novel problems. These results clearly demonstrate the existence of higher learning abilities in at least some avian species. They also raise several issues about the evolution of cognitive abilities in animals, which further research with birds can help to resolve.

References

Balda R.P. - Z. Tierpsychol., 1980, 52, p. 346.

Bessemer D.W., Stollnitz F. - In: Behavior of Nonhuman Primates. Vol. 4 / Eds. A.M.Schrier, F.Stollnitz. N.Y.: Acad. Press, 1971, p. 1-58.

Couvillon P.A., Bitterman M.E. - J. Comp. Physiol. Psych., 1980, 94, p. 878-885.

Harlow H.F. - Psychol. Rev., 1949, 56, p. 51-65.

Hunter M.W., Kamil A.C. - Psychon. Sci., 1971, 22, p. 271-273.

Kamil A.C., Hunter N.W. - J. Comp. Physiol. Psych., 1969, 73, p. 68-73.

Kamil A.C., Lougee M., Shulman R.I. - J. Comp. Physiol. Psych., 1973, 82, p. 394-405.

Kamil A.C., Jones T.B., Pietrewicz A., Mauldin J.E. - J. Comp. Physiol. Psych., 1977, 91, p. 79-86.

Krebs J.R., Davies N.B. Behavioural Ecology: An Evolutionary Approach. Sunderland, MA. Sinauer, 1979.

Krushinsky L.V., Zorina Z.A., Dashevsky B.A. -Zh. Vyss. Ner., 1979, 29, p. 590-597.

Pepperberg I.M. - Z. Tierpsychol., 1981, 55, p. 139-160.

Ricciardi A.M., Treichler F.R. - J. Comp. Physiol. Psych., 1970, 73, p. 314-319.

Schusterman R.J. - Science, 1962, 137, p. 422-423.

Stettner L.J., Matyniak K.A. - Sci. Am., 1968, 218, p. 64-76.

Vander Wall S.B. - Anim. Behav., 1982, 30, p. 84-94.

Warren J.M. - In: Behavior of Nonhuman Primates. Vol. 1 / Eds. A.M.Schrier, Harlow H.R., Stollnitz F. N.Y.: Acad. Press, 1965.

Warren J.M. - J. Comp. Physiol. Psych., 1966, 61, p. 421-428.

Welty J.C. The Life of Birds. N.Y., Knopf, 1962.

Zeigler H.P. -J. Comp. Physiol. Psych., 1961, 54, p. 252-254.

HOMOLOGOUS RELATIONSHIPS IN THE CENTRAL NERVOUS SYSTEM
OF BIRDS AND MAMMALS

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Apart from the difficulties usual in this kind of studies the elucidation
of homologies between the nervous centres of birds and mammals is complicat-
ed, by a peculiar character of onto- and phylo-genesis of the brain and its
parts. In my view, four factors, interrelated to a considerable extent, play
a special role in studying homologies and yet they are insufficiently taken
into account in comparative-morphological studies of the nervous system.

1. Intensive processes of migration of nervous elements in ontogenesis.

The basic principle of ontogenetic development of the brain consists in
that neurons arise in places other than those of their localization in the
adult nervous centre (Sidman, Rakie, 1973). Several foci of proliferation are
known to exist in the vertebrate brain from which the embryonic cells migrate
to places of prospective nervous structures. Therefore, the problem of homo-
logous relationships of any brain structures cannot be solved by merely in-
dicating the single source of their origin. Migrational processes are very
complicated and insufficiently studied, sometimes they are counterdirected.
For example, the inner segment of the pale globe migrates in telencephalon
from diencephalon and a part of embryonic material for the dorsal nuclei of
the latter migrates vice versa, from telencephalon. Further more, the two-
wave process of neuroblast migration is a most characteristic feature of neo-
cortex development (Polyakov, 1965), and this is to be taken into account
when establishing homologies between this structure and the hyper- and neo-
striatum of birds.

A comparison of the acoustic system in birds and mammals demonstrates that
in the latter each level consists of a greater number of components, and each
component has a wider set of neuron forms. Neurohistological analysis has
shown that in birds the auditory nuclei of diencephalon are made up almost
entirely of highly specialized cells, rather primitive by the organization
of dendrites (Ilyichev et al., 1976). There is a special form in each nucleus
which is a kind of "visiting card" for this structure. In mammals such neu-
rons are preserved but are suppressed quantitatively by the development of
more progressive specialized elements and by migration in all nuclei of a
large number of granular, reticular and reticular-like elements which appear
to include giant neurons related to the motor system.

2. The presence of intermediate, or temporary embryonic forms in a number
of neurons.

Such forms can be consolidated as definitive ones in the same brain regi-
ons of lower animals or occur in more ancient nervous centres in different
groups of invertebrates. For example, the pyramidal neurons of layers V and
III, which are of different evolutionary age, arise, according to Polyakov
(1979), from different temporary forms, one of which ("pyramid-spindle") is
widely represented in the brain cortex of adult reptiles.

Many neurons of other brain regions proceed in their development through
temporary stages which are often expressed in an excessive formation of

dendrites and different cell shape. Similar embryonic forms were described by Zhukova (1977) for the development of large neurons of the spinal cord gelatinous substance and were termed as "neural glialike". Neurons of similar form were found in the laminary auditory nucleus of diencephalon in adult birds (Ilyichev et al., 1976), the highly specialized cells of medial part of this nucleus being more like the glial cells and embryonic glial-like stages of the large neurons of gelatinous substance in mammals. These rare in their appearance neurons are present in enormous quantities in the laminary nucleus of well locating birds (owl, harrier) and, on the contrary, are quite scarce or may even be absent from the brain of other avian species. Such cells were not found in the brain of adult mammals either.

3. Redistribution of cellular material in phylogenesis.

The intensive development of evolutionarily young brain systems, as well as essential reorganization of sensory and motor nervous centres, are accompanied by marked changes in the amount of elements involved in the formation of a particular brain division.

The possibility of comparatively "rapid" (in the evolutionary sence) transfer of cellular material from one centre or system into another is expecially clearly demonstrated during the research of the adaptive transformations of sensory systems. For example, the closely related avian species can differ in the number of the above mentioned cells of the laminary nucleus medial part to a greater extent than taxonomically remote species which are characterized by similar indices of hearing. The hen-harrier has 7000 such neurons and the steppe eagle only 1390, whereas the snowy owl and eagle owl have similar with the former number of neurons: 6600 and 7000, resp. This part of acoustic system is completely absent in the tufted penguin and well expressed in the gold-tufted penguin which belongs to the same genus (Barsova, 1980). Such instability of the whole part of sensory system suggests that material comes to the brain systems and, in case it is less required, migrates to other centres and transforms therein into new forms. It is as yet completely unknown from what sources these cells take their origin in the owls and harriers and into what forms they transform in the brain of those birds where the laminary nucleus medial part is greatly reduced or absent.

The most important redistribution of embryonic material in the evolution of the central nervous system of higher vertebrates takes place in telencephalon and determines a parallel and independent development of neocortex in mammals and that of hyper- and neostriatum in birds. In 1969 Karten proposed his model of development of telencephalon in birds and memmals from hypothetic, common to amniotes, telencephalon. It is based on hypothesis on a possibility of two ways of migration and development of cellular elements from a single source, dorsal hippopallial tuber of reptiles: in the direction of cortical regions (mammals) and in the direction of striatum (birds). The reptiles are, however, a complex, most likely, polyphyletic class comprising crocodiles and turtles which are of particular interest from the viewpoint of comparison with birds and mammals respectively. Even the telencephalon of these animals is characterized by a great difference in the development of striatum and neocortex. Seven basic features of similarity are common to the turtles and mammals. The crocodiles are closely related to birds, expecially to their primitive representatives. Before we begin to compare the telence-

phalon of mammals and birds, it is necessary to solve the problem of homologies of the cortex regions between the reptiles and mammals which remains as yet open. Although turtles and crocodiles represent different directions of development of the brain hemispheres, they differ in the organization of telencephalon and, the more so, of cortex to a much lesser extent than birds and mammals.

4. The unity of principles of neuronal net organization.

Karten (1969) and his followers compare quite correctly, in the functional aspect, areas of visual and acoustic projections in the avian neostriatum with corresponding areas in the mammalian neocortex. But functional similarity is that by analogy, rather than by homology; therefore, further speculations of these authors on direct comparison of the granular fields of striatum (fields A and L), where visual and acoustic afferents terminate, with layer IV of visual and acoustic afferents terminate, with layer IV of visual and acoustic cortex of mammals, are incorrect. The isolation of layer IV as something structurally and functionally independent of the whole section of cortex with which it is connected by the course of cortical plate development seems very artificial. The granular character of layer IV is a feature of not only these projection cortical fields but of the whole retrocentral division of neocortex (Bogoslovskaya, Polyakov, 1981). Besides, the granular character, as well as the layered structure, is inherent in general to the nervous centres of diverse origin which are related to visual perception (Zavarzin, 1950).

The ideas of Karten on a single embryonic source of development of the divisions of avian hyper- and neostriatum and mammalian neocortex appear to agree with the facts. But he considers the marked differences in the ultrastructure of cortex and striatum as random and insignificant, while I think they represent a regular result of different ways of development of a considerable part of telencephalon. These two independent and parallel ways became distinct in morphological aspect already at the level of reptiles. A study of the fine neuronal organization of avian striatum (Bogoslovskaya, Polyakov, 1981) allows me to suggest that birds have a constructive variant of structural organization of the brain higher centres, other than mammals.

R e f e r e n c e s

Barsova L.I. - In: Sensory systems and a brain of birds. Moscow: Nauka, 1980,p.165-180

Bogoslovskaya L.S., Poljakov G.J. Ways of the morphological progress in nervous centers of the higer vertebrates. Moscow: Nauka,1981. 159 p.

Ilyichev V.D., Bogoslovskaya L.S., Barsova L.I. - Zool. J.,1976,55,N1, p. 89-102

Karten H.J. - Ann. N.Y. Acad. Sci.,1969,167,164-179.

Poljakov G.J - In: The development of the child's brain. Moscow: Meditzina,1965,p.22-52.

Poljakov G J Entwicklung der Neuronen der menschlichen Grosshirnrinde. Leipzig: VEB G.Thieme,1979.320S.

Sidman R.L., Rakic P. - Brain Res.,1973,62,p.1-35.

Zavarzin A.A. The selected works. Moscow;Leningrad: Publishing house Acad. Sci. USSR,1950,3.320 p.

Zhukova G.P. Neuronal structure and interneuronal connections in the brain stem and the spinal cord.Moscow: Meditzina,1977.143p.

# STUDY OF CONSCIOUS ACTIVITY AND ITS MORPHOLOGICAL BASIS IN BIRDS

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The views on birds' behavior have undergone radical changes in the course
of the last few decades. Up to the thirties the prevailing opinion spelled
that a less pronounced development of the cerebral structures, corresponding
to the cortical structures of the mammals' brain, points to a primitive cha-
racter of their behavior. According to the widespread opinion of physiolo-
gists existing at that time birds possess the inherent type of highly develo-
ped complex instinctive forms of behavior while their intellect is restric-
ted (Herrick, 1924). However, as it was proved by the subsequent investigati-
ons of ethologists and comparative physiologists, an extremely pronounced di-
versity and behavioral flexibility in birds can hardly be distinguished from
those in the behavior of mammals (Thorpe, 1956).

It turned out to be paradoxical that in spite of the fact that birds dis-
play very flexible forms of behavior their cerebrum exhibits an entirely dif-
ferent morphological structure than is the case in the event of mammals. The
laminated new cortex detected in all representatives of mammals is nonexis-
tent in birds. Nevertheless birds appeared to be capable of assimilating dif-
ferent complicated forms of training and solving the problems which require
a certain aptitude for correlation and elementary forms of abstraction.

The overwhelming majority of investigations are carried out with pigeons
and hens. However, the birds belonging to the Corvidae family considerably
excel pigeons as well as some other mammals in their aptitude for an exact
time discrimination (Powell, 1972). In Corvidae it is possible to obtain the
trained reflexes for much greater time intervals than in pigeons. In dis-
tinction to pigeons, the birds representing the Corvidae family do not need
any additional stimuli to produce the correct responses (Powell, 1973,1974).
According to the data presented by Gossette (1966) magpies considerably ex-
cel chicks and quails in their capability to readapt the formed habits. From
Koehler's investigations (1952, 1954) it follows that pigeons could operate
with the quantities amounting to 5 whereas ravens and parrots – within the
range of 7. In his experiments performed on jackdaws and magpies Friede
(1972) discovered that these birds are capable to operate with such notions
as "likeness – distinction".

Kamil and his collaborators (Kamil, Hunter, 1970; Kamil et al., 1973)
studied the complicated form of training for blue jays (Cyanocitta cristata)
and mynas (Gracula religiosa). For a long period of time these birds were
trained with a view to create in them gradually numerous discrimination
reactions, and little by little they learned to pick over the correct se-
lection. The authors appraise such a behavior as formation of "training de-
velopment" and believe that this characteristics of corvidae birds may be
compared with those of cats, squirrel monkeys and monkeys relating to the
Cercopithecidae family.

Our investigations reveal that judging by the level of their elementary
conscious activity Corvidae hold quite a prominent position.

According to our plan of work we carry out the comparison study of conscious activity in the representatives of different taxonomic groups of vertebrates (1958-1977). Proceeding from the self-evident assumption spelling that our actual habitat is represented by the objects, phenomena and laws forming the basis of the environment, it becomes possible to give a definite determination for the conscious activity: it is a capability to realize the laws which form the foundation of the medium structural organization. A clearly defined selection of the behavioral acts formed on the basis of an aptitude for grasping the laws combining the objects and phenomena of the environment made it possible to give not only an unambiguous determination of this form of higher nervous activity but also to carry out its unprejudiced investigation.

This investigation showed that the behavioral acts formed on the basis of conscious activity can be realized by the representatives of certain taxonomic groups of vertebrates already in the first formulation of test.

The ability of animal to make its decision at once without any preparatory behavioral training represents a unique quality of conscious activity as a fine adaptive mechanism to the multiform habitat.

The effect of realization of a conscious act in animals is revealed as an extremely frequently observed pronounced neurosis which has a distinct electrographic manifestation. Neuroses develop despite the fact that the solved test may prove to get a favorable confirmation.

As a result of our observations of animals' behavior in natural conditions of their habitat we have come to the conclusion that it is possible to make out several parameters of conscious activity. We found it possible to differentiate three forms of behavior which are executed by man as well as by animals on the basis of application of empirically assimilated laws of nature that can be used for estimating the level of conscious activity in the animals relating to different taxonomic groups.

The first form is associated with animals' aptitude for extrapolation(projection of a known function on a line segment into an outside area). The behavioral acts realized on the basis of extrapolation can be objectively registered and given a quantitative assessment. The general principle, forming the basis for the conducted experiments, implies that the animal must find the bait moving rectilinearly at a constant rate. The primary line segment of motion of the stimulus is accomplished within the visual field of the animal; then the bait disappears behind a barrier. With such a form of the experiment the animal can define the motion direction of the desired stimulant behind the barrier if it is capable of extrapolation.

The second form of behavior, offering a means of estimating the level of conscious activity, is the ability of animals to operate on the empirical dimensions of figures. The animals provided with adequately high-differentiated cerebrum can understand that a volumetric bait cannot be held inside a place figure; it can be held only inside a volumetric figure and thus be removed from one space area to another.

The third form is associated with the ability to construct a vector, determine the value of space rated motion of the subject(Fig.1).A man or an animal to be tested is suggested to make a choice in a set of cylinders (usually 12)
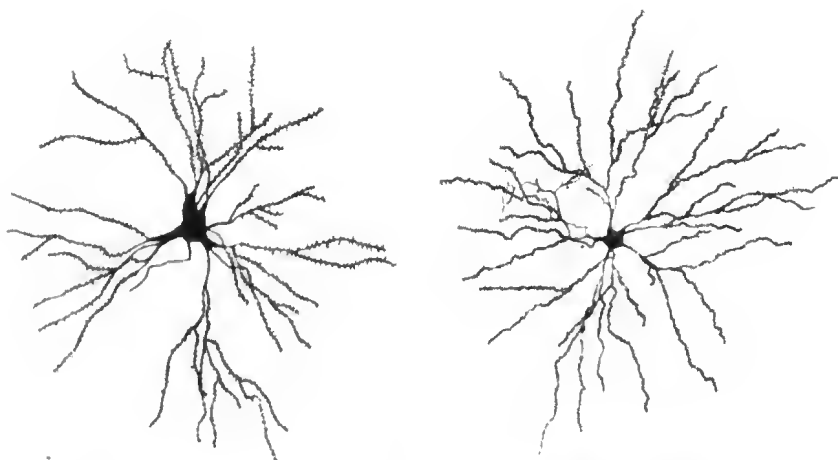
F i g. 1. Dolichoaxonic neurons from the birds' neostriatum: the Crow (right-hand) and the Pigeon (left-hand)

arranged in one line, the bait being placed under one of them. As a rule the bait is placed in the first, then in the second, the third and so on cylinders. In fact after the first two choices the tested animal obtains the required sufficient information allowing it to assess the regularity determining the displacement of the bait under the cylinders. In the event of men the criterion for the correct solution of this task spells that three cylinders in which the bait is replaced should be removed in succession without mistakes (Krushinsky, Popova, 1978). Our experiments proved that corvidae to a certain extent reveal their capability to solve this difficult task; however, in most cases they can realize the detected regularity only in the form of "incomplete" solutions. This fact can be easily explained taking into consideration that the presented task proves to be difficult even for men. With due regard for such "incomplete" solutions in the first test 23% of the birds graspsd the logical structure of the task, and in the repeated tests the correct solutions were registered for 32% of the birds. In individual cases the corvidae solved the presented task reaching the criterion which was introduced in the experiments with men. In the first test such solutions were detected in one bird, in the second - in two birds (Krushinsky et al., 1982).

All the three forms of the experimental investigation may be used for estimating the level of conscious activity in different taxonomic groups of vertebrates.

The experiments carried out by the author in cooperation with a group of his collaborators have shown that pigeons hold a low level of conscious activity. They may be compared with mouselike rodents, and yet their position in respect to the hare's species is somewhat lower. Judging by the level of conscious activity hens hold a slightly superior position than pigeons and are approaching to the hare's species. The behavior of birds of prey (common kestrels, merlins, buzzards, steppe eagles and perns) may be compared with the one of the hare's species, though perns display a more developed ability to extrapolation than the other birds of prey which we have studied. By the level of development of their conscious activity the corvidae (crows, hooded

crows, rooks, magpies and jackdaws) may well be compared with the predatory mammals belonging to the family of doglike species, and they are even superior to them in the solution of certain tasks so that they are approaching to brown bears, dolphins and some monkey species. The investigations conducted by us are in full agreement with the data of the ethologists who have come to the conclusion on a high-grade plasticity and diversified behavior of birds that can be compared with the behavior of higher mammals.

The fact that the birds which do not possess the inherent new cortex reveal the ability to solve the same problem as the predatory mammals with a well developed new cortex makes it possible to conclude that the elementary conscious activity is realized not necessarily with the assistance of the new seven-layer cortex. In this connection we are facing a new problem:which particular structures of cerebrum are responsible for realization of this complicated form of behavior in birds? When examining this problem most of the investigators point to the complex of basal nuclei that make up the structure of dorsal eminence called Wulst. This structure consists of Hyperstriatum accessorium, Hyperstriatum dorsale and Nucleus intercalatus hyperstriate, and it is covered with a thin corticoid layer. It is supposed that wulst may be considered as a single morphological structure compatible with the neopallium of the lower mammals (Kappers, 1928). Karten and his collaborators (Karten, 1969; Karten et al., 1973) made a substantial contribution to the understanding of functional activity. They specified the homology of a number of structures both in mammals and birds. It was shown that the main route from thalamus to wulst is similar to the geniculostriatal route of mammals. At the same time it was also shown that wulst represents the projection zone of the visual analyzer. In Karten's opinion the difference between wulst and the new cortex resides in the space distribution of neuronic groupings rather than in the properties of individual neurons or neuronic populations which is expressed through the absence of seven-layer cortex in birds. Karten's opinion is confirmed by the investigations of E.D.Morenkov and Do Cong Hun (1975) who have come to the conclusion that along with certain other functions wulst is involved in the visual control of the performed motor reactions. It follows that is spite of the specific nature characterizing the structure of the birds' brain it has the same basic functional systems which despite the lack of the sevenlayer cortex provide its complicated functional activity.

So we are facing the problem on a comparative morphophysiological examination of the neuronic organization of the brain of birds displaying different levels of conscious activity.

Comparison between the structures of paleostriatum and neostriatum revealed the existence of certain distinctions in the birds displaying different levels of their conscious activity (Columbae and Corvidae). When comparing the neurons of plaeostriatum with those of neostriatum in crows as well as in pigeons, L.P.Dobrokhotova (1969) revealed that the morphology of dolichoaxonic neurons of neostriatum is more complicated than it is in paleostriatum. The average number of dendritic endings in paleostriatum is 17-18, and the number of dendritic trunks is no more than 3. In neostriatum the average number of dendritic endings of dolichoaxonic cells is 27-28, and the number of dendritic trunks amounts to 5.

The correlation of paleostriatum and neostriatum neurons in crows and pigeons has shown that in these species similar groups of cells exist inside the limits of every sector of the brain. In this case one can observe certain distinctions in the fine structure of neurons in crows and pigeons. For example, in crows the bodies of dolichoaxonic cells have an angular form, in pigeons this form is more rounded. In crows the dendrites of neurons proved to be thinner and more winding than those of pigeons; the trunks of neurons are straighter (they often have varicose enlargements) (Fig.2).

The dendrites of brachyaxonic neurons are especially thin in crows;their distal fragments become drastically thinner acquiring a clearly defined form. Among the crow's dolichoaxonic neurons of neostriatum one can find some dendrites studded with an extremely thick cover of small spines. In distinction to crows the neurons of pigeons have a coarser structure: their dendrites are thicker, less winding and covered with large-sized widely spaced small spines. As a rule they have a primitive rod-shaped or hooked form and are provided with varicose enlargements (Dobrokhotova, 1981).

Crows have a more perfect and multiform system of interneuronic contacts as compared with the system of pigeons, and this may represent the very type of morphological structural basis which specifies a different level of conscious activity in these birds.

L.S.Bogoslovskaya and G.I.Polyakov (1981) have come to the analogous conclusions. They have failed to detect any distinctions between the densely ramified neurons, having very thin not high small spines, in different sectors of hyper- and neostriatum of corvidae. At the same time such type of nerve cells have never been detected in pigeons.
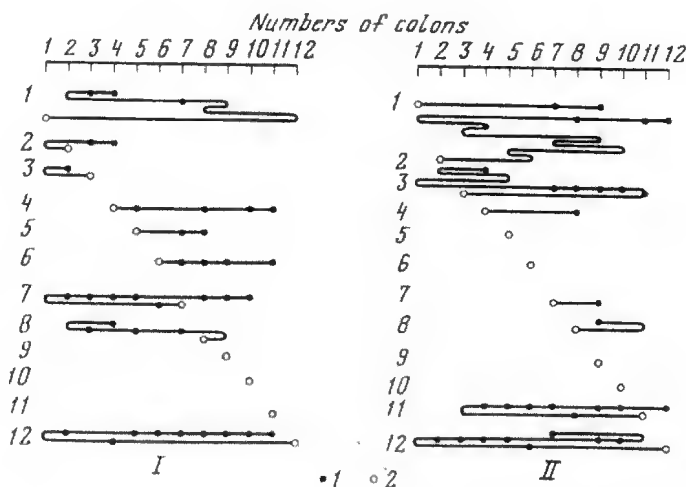


F i g. 2. Scheme for the solution of a task on determining the regular character of rate of motion of the bait by Corvidae

I - Correct solution of the task; II - "Incomplete" solution of the task; 1 - selection of an empty cylinder; 2 - selection of a cylinder containing the bait

The importance of different structures of the birds' brain in the mechanisms of their conscious activity was studied with the method of extirpations. The use of this method made it possible to reveal the role of different sectors of brain in the realization of different forms of complicated behavioral acts. It was shown that the old cortex (archicortex) is first of all related to the memory as well as to such forms of behavior which are based on training. The relative development of these cortical hippocampal sectors of the birds' brain is low: they are substantially reduced as compared to the reptilian cortex (Kappers, 1928; Huber, Crosby, 1926), and by their cellular structure reveal only slight distinctions from the subcortical formations.

In birds the old cortex occupies the dorsal and medial surfaces of hemispheres. It is isolated from the other brain structures by the ventricle cavity and differentiated in the denticulated fascia, the ammon formation and the corticoid layer.

N.L.Krushinskaya (1963, 1966) investigated the role of the old cortex in the realization of higher nervous activity in birds. She obtained the clearly defined results pointing to the fact that this structure is related to the memory to a greater extent. The investigations were conducted on nutcrackers which are very keen in locating the sites where they stored up their cedar nuts. In the case of removal of their hippocampel cortex these birds lost their ability to discover the sites of their stores. The conducted experiments give the ground to draw a conclusion that the old cortex plays as important role in the mechanisms of the birds' memory.

We have obtained coherent results in studying the role of wulst in the realization of conscious activity of birds. This complicated integrated function of brain is certainly associated with wulst representing an analog of the cortex in the end brain of mammals. The role of this structure in the power of birds behavioral plasticity becomes especially evident when comparing the neuronic organization of the pigeons' brain with the one of the birds belonging to the corvidae family distinguished by the high level of their conscious activity.

Quite definite results for the role of wulst in the behavior were obtained by the investigations based on the removal of this structure in the representatives of the species of birds exhibiting the greatest plasticity in the forms of their behavior. The destruction of wulst in corvidae produces drastic changes in their adaptive behavior which should be regarded as reasonable.

The destruction of wulst representing the sector of brain regarded as the basic integrating structure of the highest forms of birds' behavior resulted for corvidae in the loss of their ability to extrapolation. Instead of the adequate solutions of the presented problem one can observe certain stereotypic inadequate forms of behavior (Zorina, Popova, 1976; Zinov'eva, Zorina, 1976; Zorina, Fedotova, 1981).

The deterioration of corvidae's ability to the correct solution of an extrapolation problem is revealed to a greater extent in the case when these birds displayed the required experience to solve it prior to the operation. It should be noted that after the destruction of archicortex in Corvidae no changes in their ability to the solution of the presented problem have ever been detected. It is therefore safe to say that in birds the ability to ex-

trapolation, which is regarded as one of the most important criteria for the level of conscious activity, is not interrelated with the old cortex of brain.

Quite a different picture is observed when we deal with hens which are practically incapable of solving the tests presented for determining the level of their conscious activity. No significant changes can be detected in the behavior of these birds after their wulst is removed.

In case of multiple training with the extrapolation test the operated hens along with the unoperated ones could gradually learn to cope with its solution. However, the removal of the old cortex in the hens resulted in deterioration of their learning ability to solve a test on extrapolation. These data are consistent with the above-mentioned experimental investigations carried out by N.L.Krushinskaya and spell that the old cortex is interrelated with the memory.

Thus as follows that the data presented here enable us to suggest that different forms of birds' behavior are based on different morphophysiological mechanisms. The acts of behavior, that are formed due to the leading effect of memory, are interrelated with the old hippocampal cortex. Its destruction causes a disorder in the ability to memorize or any training perception. The complicated and extremely pliable forms of birds' behavior, which are regarded by us a conscious forms, must be related to a specific formation named as wulst; this peculiar formation is inherent only in birds. In its function this formation is similar to the mammals' cerebral cortex and its higher integrative center, that is the prefrontal sector. For this reason similar results can be observed after the destruction of wulst in corvidae as well as after the extirpation of prefrontal cortex in the mammals displaying a sufficiently highly developed level of their conscious activity which was demonstrated by O.S.Adrianov and L.N.Molodkina (1974) in the experiments when they removed the prefrontal cortex in the predatory mammals (cats).

The presented data enable us to express certain ideas on possible courses of evolution of the birds' end brain and on the peculiarities of their behavior. Considering the problem of evolution of the reptilian end brain I.N.Filimonov (1955) pointed to the fact that it proceeded along the two opposing courses: in the case of birds it took the direction of dominant development of the central nodes; in mammals - the development of cortex. In the functional aspect the evolution of the birds' brain revealed itself in a greater development of their instinctive reactions whereas in mammals the acquired priority became evident in their "plastic functions".

In our opinion Filimonov's concept of the course of evolution of the birds' brain may be extended. The evolution of the birds' brain as well as their behavior proceeded at least along two courses. The first course is represented by the evolution of the old cortex. Despite the reduction of the lateral and dorsal cortexes, present in reptiles, the old primordial hippocampal cortex has a clearly pronounced character in birds, and as it was already mentioned above it is interrelated both with their training perception and memory.

It may be safely assumed that with well developed optic lobes in birds the old cortex secures possibilities for migrations, locating the sites of their nesting areas, finding the clutches and accomplishing numerous other forms of behavior carried out on the basis of orientation and training.

However, the most prominent feature characterizing the birds' brain and their behavior in the course of evolution since reptiles is a powerful development of basal nuclei representing the main morphological structure of the brain which is related to the higher functions of nervous activity (Kurepina,1981).

The investigations carried out in our laboratory reveal that in such a highly organized family of passerine species of birds as corvidae the dorsal strial enlargement plays a leading role in the realization of those behavioral acts that may be determined as conscious.

This suggests that in addition to the routine instinctive reactions,which show up in the process of electrostimulation of the deep turncal structures of the brain in birds (R.Holst, U.V.Sant Paul, 1963), there exist two different forms of adaptive behavior interrelated with different structures of the brain. One form is related to the old cortex providing the functions of memory, the other form is related to the striatal structure which is specific for the birds' brain and considered as an analog of the new cortex of mammals. This structure provides the birds belonging to certain taxonomic groups with a possibility to realize complicated and extremely plastic acts of behavior which may be considered as conscious.

Despite the fact that the morphophysiological evolution of brain and the behavior of birds and mammals proceeded along the different courses in their development, it turns out that the final results of the complicated and most pliable forms of behavior are similar.

The presented scheme of interrelations between the above-mentioned systems of brain in the process of realization of a conscious act offered certain opportunities for the specific physiogenetical study of conscious activity. The scheme made it possible to specify this conscious activity as an independent function of brain which has a fundamental distinction from the instincts or any forms of training and at the same time provides the basis for the most prominent functional pathologies of brain.

In spite of the fact that we specify the acts of behavior realized on the basis of conscious activity as an independent form of behavior, differing from the instincts or conditioned reflexes, in the actual life all the three components of behavior are in constant interaction with each other. However, in the animals belonging to different taxonomic groups their relative significance is different. The greatest relative significance of conscious activity is certainly inherent in man. The social and labor-management relations, forming the social basis for the human society, are regulated by conscious activity with the assistance of speech.

SUMMARY

Opinion on the plasticity of birds behavior has changed significanty during last 10 years. In spite of slight development of cortex and absence of neocortex at all in birds, according to the level of highest nervous activity, some taxonomic groups of birds can be compared to such mammals as dogs, bears and primates. The highest behavioral prasticity is characteristic for Corvidae birds. It could be regarded as reasoning ability. The level of development of this form of highest nervous activity is correlated with comp-

lexity of their intragroup relations with appearence of personally directed vocalization and other complex behavioral forms, such as directed manipulating by things, and so on. The complexity of morphological organization of brain corresponds to behavioral plasticity. It is shown, that elementary reasoning ability is more developed in Gorvidae birds, than in doves. The neuronal organization of Neostriatum in Corvidae birds allows more fine analysis and proceeding of information in brain, than such in doves. Thus, in spite of difference in evolutionary ways of brains development in comparison with mammals, birds brain has all necessary neurophysiological mechanisms to cover their high level of behavioral adaptability.

R e f e r e n c e s

Adrianov O.S., Molodkina L.N. - J. Of Higher Nervous Activity, 1969, 19, N 4, p. 593-601.

Bogoslovskaya L.S., Polyakov G.I. Routes of Morphological Progress of Nerve Centers in Higher Vertebrates. Moscow: Nauka, 1981.

Dobrokhotova L.P. - In: The collection of "XXII Meeting on the Problems of Higher Nervous Activity". Abstract and summaries of reports. Ryazan, 1969, p. 87.

Dobrokhotova L.P. - Proceedings of the USSR Ac. Sc., 1981, 257, N 1, p. 242-244.

Filatov D.P. Comparative Morphological Course in the Mechanism of Development, Its Subject, Goals and Routes. Moscow; Leningrad: USSR Ac. of Sc. Publishing House, 1939.

Filimonov I.N. - In: Neurology Guide. Pt I. Moscow: Medgiz, 1955.

Friede A. - Z. Tierpsychol., 1972, 30, N 4, p. 383-404.

Gossette R., Gossette M.G., Riddell W. - Anim. behavior, 1966, 14, p. 560-564.

Holst E., Saint-Paul U. - Anim. Behavior, 1972, 11, p. 1-20.

Huber G.C., Crosby E.C. - J. Comp. Neurol., 1929, 48, p. 1-222.

Kamil A.C., Hunter M. - J. Comp. Physiol. Psychol., 1970, 73, N 1, p. 68-73.

Kamil A.C., Jones T.B., Pietrewicz A., Mauldin J.E. - J. Comp. and Physiol. Psychol., 1977, 91, N 1, p. 79-86.

Kappers A.C.U. - Acta Psychiat. a. Neurol., 1928, 13, N 3, p. 113.

Karten H.I. - Ann. N.J. Acad. Sci., 1969, 167, p. 164-179.

Karten H.I., Hodos W., Nauta W.J., Revzin A.M. - J. Comp. Neurol., 1973, 150, N 3, p. 253-277.

Koehler O. - Bull. Animal Sci., 1950, 9, p. 16-23.

Koehler O. - Freiburger Dies Universitatis, 1957/1958, 6, S. 97-116.

Krushinskaya N.L. - J. of Higher Nervous Activity, 1963, 13, N 6, p. 1077-1086.

Krushinskaya N.L. - J. of Evolutionary Biochemistry and Physiology, 1966, 2, N 6, p. 563-568.

Krushinsky L.V., Zorina Z.A., Dobrokhotova L.P. et al. - Ornithologia, N 17, p. 22-35.

Krushinsky L.V., Popova N.P. - Proceedings of the USSR Ac. Sc., 1978, 240, N 4, p. 997-999.

Kurepina M.M. Animals' Brain. Moscow: Nauka, 1981.

Morenkov E.D., Do Cong Hun. — In: Materials of the All-Union Congress of Physiologists, Tbilisi, 1975.

Polyakov G.I. The Problem of Origin of the Brain Reflex Mechanisms. Moscow: Meditsina, 1964.

Powell R.W. — The Auk, 1972, 89, p. 738–742.

Powell R.W. — J. Comp. Physiol. Psychol., 1974, 86, N 4, p. 736–746.

Thorpe W.H. Learning and Instinct in Animals. L., 1958.

Zinov'eva I.B., Zorina Z.A. — J. of General Biology, 1976, 37, N 4, p. 600–607.

Zorina Z.A., Popova N.P. — J. of Higher Nervous Activity, 1976, 26, N 1, p. 127–131.

Zorina Z.A., Fedotova I.B. — J. of Higher Nervous Activity, 1981, 31, N 1, p. 185–187.

# INTRODUCTION TO THE DIFFUSIVE EXCHANGES AND
# WATER RELATIONS OF AVIAN EGGS

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## INTRODUCTION

Ornithologists have always been interested in bird eggs and since the middle 1700's increadible numbers of bird eggs have been collected and catalogued by amateur öologists. These extensive collections were utilized by the great German amateur Max Schonwetter in his monumental descriptions of egg dimensions (1960-78) and by the American amateur, Frank Preston (1969) in his quantification and comparative study of egg shapes. Ethologists and ecologists have always been interested in avian reproduction and incubation but one of the first such studies to include consideration of physiological aspects of incubation and eggs in a wild species, was the comprehensive study of the functional aspects of incubation in the Herring Gull (<u>Larus argentatus</u>) by the Dutch ornithologist Rudolph Drent (1970).

At about the same time the first in a series of landmark papers dealing with the respiratory exchanges of chicken eggs was published (Wangensteen, Rahn, 1970/71). The man whom I consider to be the father of "Physiological Oology" is Dr. Hermann Rahn of the United States. Dr. Rahn and his two closest collaborators, Dr. Charles Paganelli of the U.S. and Dr. Amos Ar of Israel were awarded the Coues Award by the American Ornithologists Union in 1981 for their "pathbreaking insights" into the physiology of bird eggs (Anon, 1982).

The purpose of this paper is to introduce the basic concepts and relationships in the area of water balance and to mention some current areas of interest. Avian embryos obtain the energy required for their development aerobically: that is they must exchange oxygen and carbon dioxide with their environment. These gases diffuse through pores in the shell (Wangensteen, Rahn, 1970/71). Pores in eggs of different species have a wide variety of shapes (Board et al., 1977). Eggs lose water by diffusion through these pores because eggs are usually incubated at temperatures which are higher than the temperature of the surrounding air. The rate at which an egg loses water is a function of two factors: the first factor is the gradient or the difference in vapor pressure between the air inside the egg and the air surrounding the egg; the second factor, conductance, can be thought of as the ease with which water vapor escapes from the egg.

The following equation relates the rate of water loss ($\dot{M}_{H_2O}$ - with units of mg per day) to the gradient ($P_{A_{H_2O}} - P_{I_{H_2O}}$) and the conductance ($G_{H_2O}$):

$$\dot{M}_{H_2O} = G_{H_2O} (P_{A_{H_2O}} - P_{I_{H_2O}}) \qquad (1)$$

The rate of water loss ($\dot{M}_{H_2O}$) is equal to the rate of weight loss (Drent, 1970). This is because there is no net loss of weight due to exchange of res-

piratory gases in bird eggs. Therefore, if one measures the rate of weight loss one knows the rate of water loss. $P_{A_{H_2O}}$ is the vapor pressure (in torr) in the gas inside the egg and $P_{I_{H_2O}}$ is the vapor pressure in the air surrounding the eggs. Conductance has units of mg per day-torr. It is determined by measuring the rate of weight loss under conditions where the gradient is known, normally in a desiccator at 25°C (Ar et al., 1974).

Conductance is partially determined by the number, length and area of the pores in the shell (Wangensteen, Rahn, 1970/71). These morphological factors are determined at the time the shell is laid down in the shell gland. Therefore, in most species, conductance to water vapor is constant throughout incubation. The only exception to this is an increase in conductance during early incubation in the eggs of some small passerines (Carey, 1979; Hanka et al., 1979). Since conductance is constant, the rate of water loss in natural incubation is nearly constant and eggs experience a nearly linear decrease in weight from the time incubation commences until the egg is pipped (Drent, 1970). The loss of weight leads to the formation of the air cell, a gas filled cavity at the blunt end of the egg.

The rate of water loss ($\dot{M}_{H_2O}$) varies in a regular way with initial egg weight (W, the weight of the egg when freshly laid) according to the equation (Ar and Rahn, 1980):

$$\dot{M}_{H_2O} = 13.2 \ W^{0.75} \tag{2}$$

An even more useful generalization is obtained by expressing the total water lost during incubation as a fraction of initial egg weight. Total water lost is estimated (Rahn and Ar, 1974) by multiplying the rate of water loss ($\dot{M}_{H_2O}$) by the length of the incubation period (I, in days):

$$F = \dot{M}_{H_2O} \times I/W \tag{3}$$

Since this equation includes the length of the incubation period (I) it is important to note that there is a considerable amount of variation in incubation period between species laying eggs of the same weight (Rahn and Ar, 1974). For eggs of any given weight there is nearly a two-fold range in incubation periods in different species. Combining this fact with equation (3) one might expect to find a considerable amount of interspecific variation in fractional weight loss resulting from differences in incubation period. But this is not the case. As shown in Figure 1, there is some variation in mean fractional weight loss between different species but the average fractional weight loss for most species falls reasonably close to 15% of initial egg weight (Ar, Rahn, 1980). This important generalization, first reported by Rahn and Ar (1974), leads one to ask: Why is there less variation in fractional weight loss than one might expect? The answer to this question is, quite simply, that the rate of water loss is adapted to the length of the incubation period (Ar, Rahn, 1980). If we compare two eggs of the same initial weight, the egg with the longer incubation period loses weight more slowly. The precise nature of this relationship is given by the equation (4).

$$\dot{M}_{H_2O} = 0.15 \ W/I \tag{4}$$
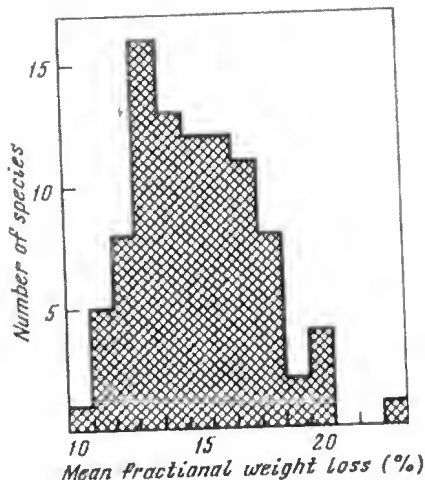
This relationship is one of the most fundamental in all of egg physiology. It is also an interesting biological phenomenon because it describes a physiological process whose rate is not only proportional to the weight of the organism but also inversely proportional to a time parameter, the incubation period. Many physiological and morphological parameters of avian eggs exhibit this complex relationship between egg weight and incubation period and, I believe, all of these relationships ultimately are linked to this one: the necessity of losing about 15% of the initial weight during incubation.

Obviously, the next question to ask is: how is this relationship achieved? If we recall the physics of the process (equation 1), we can see the possible answers: if the rate of water loss is inversely proportional to incubation period, the conductance or the gradient must also be inversely proportional to incubation period. It appears from several studies that the gradient is about the same in most species with a value of about 34 torr (Ar, Rahn, 1980). Therefore, we are not surprised to find (Hoyt, 1980) as originally predicted by Rahn and Ar (1974) that conductance is related to both egg weight and incubation period:

$$G_{H_2O} = K_G \ W/I \qquad (5)$$

We can rearrange this equation to give:

$$K_G = G_{H_2O} \ I/W \qquad (6)$$

We can calculate the value of the Conductance Coefficient ($K_G$) for any species for which we know egg weight, conductance and incubation period using equation (6).

Ar and Rahn (1978) report a mean value of this coefficient for 90 species of 5.13±0.86 (SD). If we substitute this mean value into equation (5) we have a good equation with which to predict the conductance of any egg for which we know weight and incubation period:

$$G_{H_2O} = 5.13 \ W/I \qquad (7)$$

It is interesting to note that there is some interspecific variation in the value of this coefficient. Figure (2) includes values of $K_G$ which differ rather markedly from 5.13. These eggs appear to be adapted to extreme environ-
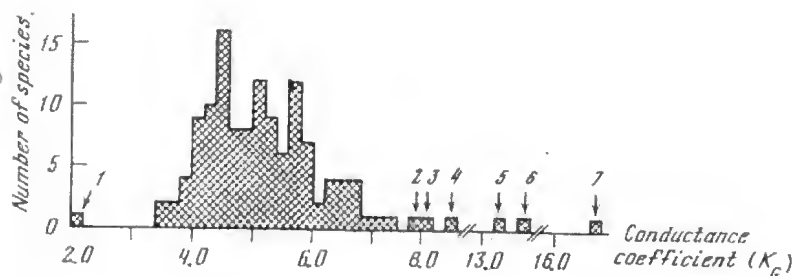
F i g. 2. A frequency histogram of mean Conductance Coefficient ($K_G$ = $G_{H_2O} \cdot I/W$) for 129 species of bird eggs. The species with high values are, presumably, adapted to humid environments and species with low values to desiccating environments

| | | Source[*] |
|---|---|---|
| 1. | <u>Anser indicus</u> (Bar-headed Goose) | |
| 2. | <u>Dendrocygna autumnalis</u> (Red-billed Whistling Duck) | a |
| 3. | <u>Dendrocygna bicolor</u> (Fulvous Whistling Duck) | a |
| 4. | <u>Fulica atra</u> (Coot) | a |
| 5. | <u>Podiceps cristatus</u> (Great Crested Grebe) | b |
| 6. | <u>Alectura lathami</u> (Brush Turkey) | b |
| 7. | <u>Gavia immer</u> (Common Loon) | c |

[*]Sources: a) Hoyt et al., 1979; b) Loholt, 1976; c) Seymour and Rah, 1978; d) H.Rahn, pers. comm.

ments. For example, the eggs of the Bar-headed Goose (<u>Anser indicus</u>) have a very low conductance for their weight and incubation period (species 1 in Figure 2). This is probably an adaptation to nesting at high altitudes. The eggs with unusually high conductances appear to be adapted to very humid nest environments. Clearly, the best way to detect adaptations of conductance to unusual environments is to calculate the Conductance Coefficient for the eggs in question and compare this value with 5.13.

MEASUREMENT OF CONDUCTANCE

Figure (3) details and unexplained peculiarity about the measurement of conductance. These data were obtained by measuring the conductance of 35 fresh chicken eggs in a desiccator (Ar et al., 1974) on six consecutive days. The conductance measured during the first 24 hours in the desiccator averages 30% higher than the value on subsequent days. This difference is statistically significant ($p < 0.05$). This peculiarity was first noted by Ar and Rahn and for this reason, the data from the first day of the measurement of conductance have traditionally been disregarded (Hoyt et al., 1979). However, as can be seen from Figure (4), most of this change occurs during the first twelve hours. These data were obtained by weighing eggs every couple of hours during the first   day in the desiccator. This change should not be confused with the change which occurs during the first few days of incubation in the eggs of some small passerines (Carey, 1979; Hanka et al., 1979). It is my hypothesis that this change does not reflect a change in pore geometry or number, but is due to the loss of excess water from the matrix of the shell during the first few hours in the desiccator.
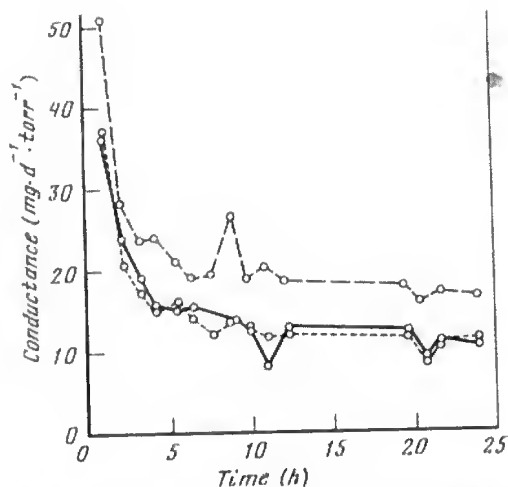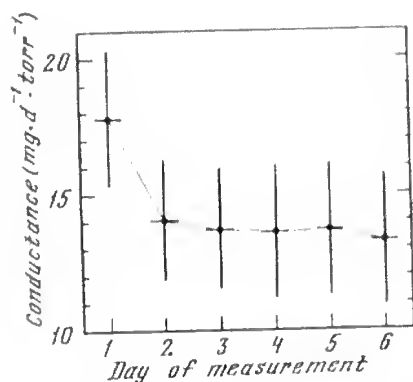
F i g. 3. Apparent changes in conductance with time in fresh Chicken (Gallus gallus) eggs. Conductance was measured in a desiccator at 25°C on six consecutive days for 35 eggs. The line connects daily mean values and vertical bars indicate one standard deviation. The mean value on the first day is 30% higher (p < 0.05) than on the second day. Because of similar changes, data from the first day of measurement are disregarded in the measurement of conductance in bird eggs

F i g. 4. Change in conductance during the first 24 hours in a desiccator in three individual fresh chicken eggs. Most of the change, which is assumed to be due to the loss of water from the shell itself, occurs during the first 12 hours

REGULATION OF NEST VAPOR PRESSURE

A topic of current controversy is the regulation of nest vapor pressure. Rahn et al. (1976) proposed the hypothesis that incubating adult birds can sense and behaviorally regulate the vapor pressure of the air in the nest. They based this hypothesis on the observation that, comparing species of terns nesting in a variety of environments, there is less interspecific variation in nest vapor pressure than there is in environmental vapor pressure. They point out that water which has escaped from the egg must subsequently escape from the nest or else the air in the nest will become saturated. Since measured nest vapor pressures are usually less than 50% of saturation, water vapor does escape from the nest. This transport of water could occur either by diffusion of water vapor through still air or by the convective exchange of drier ambient air for the moist nest air. They assumed that the later process, which they refer to as "ventilation", is the most important of the two mechanisms. They suggest that birds could permit ambient air to enter the nest by standing up and could control the amount of ambient air entering the nest by varying the number of times they stand up every hour. This hypothesis was evaluated by Walsberg (1980). He utilized a deterministic mathematical model to evaluate the influence of standing up on the transport of water vapor out of a fibrous cup nest. He concluded that even if an incubating bird never stood up there would be very little difference in vapor pres-

P i g. 5.
Frequency histogram of fractional
weight loss in individual Tern
eggs. Differences in mean values
of the two species are signifi-
cantly different (p < 0.001).
All of these eggs hatched, in-
dicating the ability to tolerate
a range of fractional weight
losses. Data from Nisbet, 1981
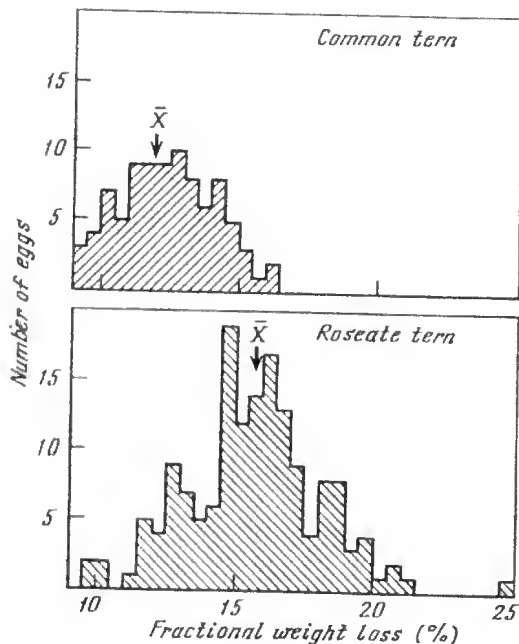
sure between ambient air and the air in the nest because water vapor could
easily diffuse directly through the walls of the nest. Data collected by
David and Carol Vleck (C.Vleck et al., in press) support Walsberg's predic-
tion, indicating a mean difference in vapor pressure between ambient and
nest air of less than 3 torr for four species of tree-nesting birds. In a
more recent study Walsberg (in press) was unable to detect any change in
parental behavior when he experimentally manipulated the vapor pressure of
nest air in two tree-nesting species by circulating saturated or dried air
through the nest. His results failed to support Rahn's hypothesis that birds
behaviorally regulate vapor pressure of nest air by standing up. However,
there have been no similar manipulative studies in ground-nesting species
where ventilation could be more important, and Rahn's hypothesis could still
be valid for these species.

INTRASPECIFIC AND INTERSPECIFIC VARIATION IN FRACTIONAL WEIGHT LOSS

Figure (5) contains data on fractional weight loss in two species of
terns (Nisbet , 1981). These data were obtained by weighing eggs to the
nearest milligram on two occasions at least one week apart. Both species were
studied at Bird Island, Massachusetts (41'40''N, 70'43'' W). Data on the Com-
mon Tern (Sterna hirundo) were collected during May and June, 1975, and those
on the Roseate Tern (Sterna dougallii) during May and June, 1980. There are
clear differences between these two species. The mean value for the Common
Tern is 12.3%±1.8 (SD) and the mean value for the Roseate Tern is 15.6%±2.4
(SD). These differences are statistically different (P < 0.001). These data
(Figure 5) also reveal a reasonably large amount of intraspecific variation
in the weight loss of these eggs. Another interesting aspect of Dr. Nisbet's
data is that they include all of the eggs he was able to obtain for his study

and virtually all of them hatched. Therefore, it seems clear that the hatchability of these tern eggs is not dramatically affected by weight losses ranging from 9 to 25%. Data from two independent studies by Dr. Kenneth Simkiss (1980) and Hoyt (1979), indicate that the ability to tolerate different levels of weight loss probably results from special physiological homeostasic mechanisms of the embryos.

THE OVERALL BUDGET OF WATER LOSS IN AVIAN EGGS

Ar and Rahn (1980) point out that the average fractional weight loss of 15% does not include water lost after the shell is pipped. This 15% represents only the water lost by diffusion through the shell. In fact, there are three phases of water loss. A small amount of water is lost between the time the egg is laid and the time incubation starts. The amount of water lost during this phase is small because there is very little, if any, difference in temperature between the egg and the surrounding air. The second phase of water loss extends from the time incubation starts until the egg is pipped. This is the diffusive phase and during this time there is a nearly linear decline in weight. The rate of weight loss during this phase is the $\dot{M}_{H_2O}$ referred to earlier. If we extrapolate this rate of weight loss to the time of hatching, we can estimate the diffusive loss (average value equals 15%). The third phase of water loss commences when the shell is pipped and ends when hatching is completed. Ar and Rahn (1980) have estimated that this paranatal water loss averages about 5%. Therefore, the total loss averages about 20%. They have suggested that the paranatal loss in precocial species may be 1-2% higher in precocial species than in altricial species. Obviously, the amount of water lost during this paranatal phase may vary rather greatly with such factors as the length of time between pipping and hatching and other species-specific differences in the actual hatching process.

SUMMARY

The rate of water loss from avian eggs is determined by the conductance and the vapor pressure gradient between the gas inside the egg and the air surrounding the egg. The amount of water lost by diffusion, which can be estimated from the product of daily rate of water loss and the length of the incubation period, averages 15% of fresh egg weight. The rate of water loss is proportional to the ratio of egg weight to incubation period because conductance is proportional to the same ratio. To detect adaptations of conductance to unusual environments is calculate the conductance coefficient ($K_G$) and compare it with the mean value of $5.13\pm0.86$ (SD). When conductance is being measured the value obtained during the first 12 to 24 hours may be erroneously high by as much as 30%. Data on rates of water loss during natural incubation in two species of terns indicate there may be significant amounts of interspecific and intraspecific variability but hatchability may not be dramatically affected by a rather wide range of weight losses. In addition to the 15% of fresh egg weight lost by diffusion, it has been estimated that another 5% are lost during the process of hatching.

R e f e r e n c e s

Anon. - Auk, 1982, 99, p. 183.

Ar A., Paganelli C.V., Reeves R.B. et al.- Condor, 1974, 76, p. 153-158.

Ar A., Rahn H. - In: Respiratory Function in Birds, Adult and Embryonic / Ed. by J.Piiper. B.: Springer-Verlag, 1978, p. 227-236.

Ar A., Rahn H. - Amer. Zool., 1980, 20, p. 373-384.

Board R.G., Tullett S.G., Perrott H.R. - J. Zool. L., 1977, 182, p. 251-265.

Carey C. - J. Exp. Zool., 1979, 209, p. 181-186.

Drent R. - Behaviour, Suppl., 1970, 17, p. 1-132.

Hanka L.R., Sotherland P.R., Taigen T.L. et al. - J. Exp. Zool., 1979, 210, p. 183-188.

Hoyt D.F. - Physiol. Zool., 1979, 52, p. 354-362.

Hoyt D.F. - Amer. Zool., 1980, 20, p. 417-425.

Hoyt D.F., Board R.G., Rahn H., Paganelli C.V. - Physiol. Zool., 1979, 52, p. 438-450.

Lomholt J.P. - J. Comp. Physiol., 1976, 105, p. 189-196.

Nisbet I.C.T. - U.S. Dept. of Interior, P.O., 1981, N 50181-0840-9.

Preston F.W. - Auk, 1968, 85, p. 454-463.

Rahn H., Ar A.- Condor, 1974, 76, p. 147-152.

Schonwetter M. - In: Handbuch der Oologie. Vol. 1 / Ed. by Wimeise. B.: Akad. Verlag, 1960-1978, p. 1-26.

Simkiss K. - J. Zool., L., 1980, 192, p. 1-8.

Seymour R.S., Rahn H. - In: Respiratory Function in Birds, Adult and Embryonic / Ed. by J.Piiper. B.: Springer-Verlag, 1978, p. 243-246.

Walsberg G.E. - Amer. Zool., 1980, 20, p. 363-372.

Walsberg G.E. - Physiol. Zool.,

Wangensteen O.D., Rahn H. - Respir. Physiol., 1970/71, 11, p. 31-45.

# RESPIRATORY GAS EXCHANGE OF AVIAN EGGS

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## INTRODUCTION

Since Schwann (1834), who showed that an adequate supply of $O_2$ is needed for the successful hatching of chicken eggs, and Hasselbalch (1900), who pioneered in the measurement of gas exchange of eggs, the study of the respiration of embryonic birds has been slowly and steadily evolving. Contributions which have been important for the understanding of the physics and physiology of this gas exchange have been provided by Romijn (1950) and in particular by Visschedijk (1968).

A powerful advancement and stimulation was then provided by Hermann Rahn and his co-workers, in Buffalo, N.Y., who started work on the physiology of gas exchange of avian eggs in 1968 (the important publications of this group from the period 1968-1980 have been compiled into a special issue edited by Rahn and Paganelli, 1981).

The work began with chicken eggs, but was soon extended to eggs of numerous wild bird species, both by the Buffalo group and by numerous other investigators more or less directly inspired by the Buffalo group. Various aspects of current research in the area were discussed in two symposia, namely in Göttingen, 1977 (Piiper, 1978), and in Tampa, Florida, 1979 (Carey, 1980a).

In this introductory report, the emphasis will be on some basic concepts of the respiratory physiology of the avian embryo.

## EXTENT OF RESPIRATORY GAS EXCHANGE

An avian egg is a self-contained life-support system providing all the nutrients, minerals and water required for the development and the maintenance of the embryo (Rahn et al., 1979). Only $O_2$, $CO_2$, water vapor and heat must be exchanged with the environment.

A chicken egg weighing 60 g will take up 6 L $O_2$ ($\approx$ 9 g) and give off 4.5 L $CO_2$ ($\approx$ 9 g) and 11 L ($\approx$ 9 g) water vapor during its incubation time of 21 days. Because the respiratory quotient is about 0.73 the mass of $O_2$ taken up closely equals that of $CO_2$ given off, and the total weight change (a decrease of about 9 g) is due to water loss. Since the avian egg shell is rigid, the water loss gives rise to the formation of an air space (air cell) between the outer and inner shell membranes at the blunt end of the egg.

In many species, the relationship between water loss and total cumulative gas exchange per mass of egg has been found to be similar. It follows from the measurements that production (and maintenance up to hatching) of a chick "costs" about 100 ml $O_2$ (equivalent to about 0.5 kcal) per g of egg or 150 ml $O_2$ (equivalent to about 0.75 kcal) per g of chick (Hoyt and Rahn, 1980; Rahn and Ar, 1980).

More accurate measurements, however, have shown that the "cost" of converting egg contents into chick tissue is lower in altricial birds as com-

pared to precocial birds, in accordance with their degree of development at hatching (Ar and Rahn, 1980; Vleck et al., 1980).

CHANGES DURING DEVELOPMENT

The metabolic rate of the embryo shows a spectacular increase during the development. In altricial bird embryos the increase of $O_2$ uptake is close to exponential, in conformity with the growth rate. In precocial birds the $O_2$ uptake tends to reach a plateau during the last days of incubation, corresponding to a reduction in the growth rate, and then rises again, to maximum value, during the labor of pipping and hatching (Vleck et al., 1980).

This increasing $O_2$ requirement is matched by an increasing performance of the gas transport system. Of decisive importance is the growth of the vascular chorioallantois on the inner surface of the egg shell. When during the latter part of the incubation time the chorioallantois has completed its growth, covering the whole inner surface of the egg shell, all the pores of the egg shell are utilized for gas exchange.

During the second half of incubation the following adaptive changes of the gas transport system have been quantitatively determined in chicken embryos: increase of chorioallantoic blood volume and flow, increase of blood hemoglobin concentration and $O_2$ affinity of hemoglobin, and increase of plasma bicarbonate concentration (Tazawa, 1980). All these changes lead to an enhanced performance of $O_2$ and $CO_2$ transport within the egg.

In spite of some increase in egg shell conductance during incubation (Carey, 1979), its limiting role in gas exchange becomes progressively more important towards the end of incubation. The diffusion limitation leads to a steady decrease of $P_{O_2}$ and increase of $P_{CO_2}$ in the egg, as reflected by measurements of the air cell gas (Romijn, Roos, 1938; Wangensteen, Rahn, 1970/71). The hypoxia developing before hatching demonstrates the limits to the gas transport performance, imposed by limited permeability of the egg shell. Thus the pipping, that is the cracking of the egg shell by the chick, and the start of lung breathing are inevitable events from the standpoint of respiration.

DIFFUSION THROUGH EGG SHELL PORES

The transfer of $O_2$, $CO_2$ and water vapor across the egg shell takes place by diffusion through the microscopic pores. The transfer rate, $\dot{M}$ ($O_2$ uptake, $CO_2$ output or $H_2O$ output), is proportional to the effective partial pressure of the gas species x across the shell, measurable as the difference between environmental air and air cell patrial pressure, $P_I-P_A$ (Wangensteen, Rahn, 1970/71; Wangensteen et al., 1970/71; Paganelli, 1980). The conductance, G, is the proportionality coefficient:

$$\dot{M}_x = G_x \cdot (P_I - P_A)_x \tag{1}$$

The diffusive conductance of the egg shell is determined by the effective total pore cross-sectional area, $A_p$, the effective pore length (approximately equal to egg shell thickness), L, and the diffusion coefficient of the gas species in air, $D_x$ (R, gas constant; T, absolute temperature):

$$G_x = \frac{A_p}{L} \cdot D_x \cdot \frac{1}{RT} . \tag{2}$$

The total functional pore area, $A_p$, results from the number of pores($N$, and the effective pore radius (4):

$$A_p = \widetilde{\pi} \, r^2 \cdot N \tag{3}$$

For a chicken egg ($N \approx 7500$, $r \approx 10$ m), $A_p$ is about 2.3 mm$^2$, a very small fraction of the total shell surface area (68 cm$^2$). Since the ratio $D_{CO_2}/D_{O_2} \approx 0.7$ is similar to the respiratory quotient $R = \dot{M}_{CO_2}/\dot{M}_{O_2}$, the partial pressure difference $P_I - P_A$ is about the same for $O_2$ and $CO_2$; $P_I - P_A$ increases from about 10 Torr (day 8) to 45 Torr (end of incubation) (Wangensteen, Rahn, 1970/71).

For a large number of bird species Ar and Rahn (1978) have shown that there exists a remarkably close inverse relationship between the specific conductance of the egg shell to water vapor (conductance $G$/egg mass $W$) and the incubation length ($I$).

$$\frac{G}{W} \cdot I = \text{const} \tag{4}$$

This relationship was established for $G_{H_2O}$(because this quantity is easily measured), but it must also be valid for $G_{O_2}$ and $G_{CO_2}$ (Ar and Rahn, 1978; Rahn, Ar, 1980). It means that slowly developing eggs have a small conductance, but as the metabolism is proportionally reduced, the $P_I - P_A$ differences at corresponding stages of development are expected to be about the same in all avian eggs.

ENVIRONMENTAL CHANGES AFFECTING DIFFUSION

Under some conditions the changes in transfer of respiratory gases as predicted on the basis of the above equations are expected to be of biological importance.

(1) Many birds lay their eggs in burrows. When the convective air movement is reduced, the $O_2$ concentration may drop and $CO_2$ may build up, due to the metabolism of the eggs as well as that of the incubating parent and that of other organisms (Pettit et al., 1982). Much greater effects, however, occur in such situations after hatching (White et al., 1978). Particularly large deviations of the environmental from the atmospheric air composition are found in the nests of the mound-building megapodids (Seymour, Rahn, 1978).

(2) At high altitude, the reduced barometric pressure has two effects (Visschedijk, 1980):

(a) The $O_2$ partial pressure decreases. To ensure sufficient $O_2$ diffusion, an increase in the egg shell conductance appears to be appropriate.

(b) The diffusion coefficient, $D$, increases for all gases, being inversely proportional to the total (barometric) pressure. This increase in $D$, therefore, would enhance water loss,and produce alkalosis by reducing $P_{CO_2}$. To compensate for this, a reduction of the conductance by decrease of the $A_p/L$ ratio seems to be appropriate.

In this conflicting situation, experimental evidence shows a decrease of the $A_p/L$ ratio in bird eggs from higher altitudes. This may be interpreted to mean that water balance (and acid-base balance) have priority over the $O_2$ supply. A prolongation of the incubation period with a reduced $O_2$ uptake rate and delayed growth rate are also found in eggs incubated at altitude (Rahn et al.,1977; Carey, 1980b).

## GAS TRANSPORT INSIDE THE EGG

The layers to be crossed by diffusion are: mineral shell, outer and inner shell membranes (fibrous networks containing air), endothelium, plasma and the membrane of the red blood cells in the chorioallantoic blood capillaries. Since the air cell is formed between the outer and the inner shell membranes, its gas analysis allows to distinguish an outer diffusion barrier (mineral shell and outer shell membrane) and an inner diffusion barrier (inner shell membrane and blood capillaries). For $CO_2$ (and $H_2O$) the major resistance to diffusion lies in the outer barrier (predominantly egg shell), but for $O_2$ the the resistance offered by the inner barrier is not negligible (Wangensteen, 1972; Piiper et al., 1980).

The next link in the gas transport system is convective transport by blood flow. The chorioallantoic capillaries receive blood from the allantoic arteries and the outflow is via the allantoic veins.

The diffusion of $O_2$ into red blood cells and the reaction of hemoglobin with $O_2$, functionally included in the inner barrier, may be important limiting processes (Wangensteen, Weibel, 1982). A particular feature in the chorioallantoic gas exchange is a large blood shunt (about 10-15%), leading to a considerable oxygenation deficit of the arterialized allantoic blood as compared to air cell gas (Piiper et al., 1980).

Moreover, since the anatomical arrangement of the embryonic circulatory system leads to mixing of arterialized blood of the allantoic veins with systemic venous blood in the embryo, the $O_2$ partial pressure and saturation in the arterial system of the embryo are expected to be further reduced (Tazawa, 1978). For example, in the chorioallantoic artery and in the arteries running to the caudal part of the body these properties are expected to be identical. In this blood ($P_{O_2}$ = 24 Torr), $O_2$ saturation has been found to be 22% only. $O_2$ saturation of arterial blood supplying the cranial part of the body may be slightly higher, due to preferential channeling of allantoic vein blood, in a manner similar to mammalian fetal circulation (Tazawa,1980). Thus the anatomical arrangement and the limited blood flow are important limiting factors for the $O_2$ supply to the tissues.

### SUMMARY

Respiratory gas exchange of the avian embryo occurs in the chorioallantoic blood capillary plexus which, when fully developed, extends over the whole inner surface of the egg shell. Diffusion of the respiratory gases through the pores of the egg shell is the predominant limiting process in exchange of carbon dioxide and important for $O_2$ exchange. The diffusive conductance of the shell, determined by the number and the dimensions of the pores, is adjusted to the metabolic rate of the embryo in such a manner that an adequate oxygen supply is insured in combination with an optimal acid-base status and water balance.

References

Ar A., Rahn H. - In: Respiratory Function of Birds, Adul. and Embryonic /
    Ed. by J.Piiper. Berlin, Heidelberg, New York: Springer, 1978, p. 293-296.
Ar A., Rahn H. - Am. Zool., 1980, 20, p. 373-384.
Carey C. - J. Exp. Zool., 1979, 209, p. 181-186.
Carey C. - Am. Zool.., 1980a, 20, p. 325-484.
Carey C. - Am. Zool., 1980b, 20, p. 449-495.
Gas exchange in avian eggs / Eds. H.Rahn, C.V.Paganelli. Buffalo: State
    University of New York at Buffalo, 1981.
Hasselbalch K.A. - Skand. Arch. Physiol., 1900, 10, p. 353-402.
Hoyt D.F., Rahn H. - Respir. Physiol., 1980, 39, p. 255-264.
Paganelli C.V. - Am. Zool., 1980, 20, p. 329-338.
Pettit R.N., Grant G.S., Whittow G.C. - Physiol. Zool., 1982, 55, p. 162-
    170.
Piiper J., Tazawa H., Ar A., Rahn H. - Respir. Physiol., 1980, 39, p. 273-
    284.
Rahn H., Ar A. - Am. Zool., 1980, 20, p. 477-484.
Rahn H., Ar A., Paganelli C.V. - Sci. Amer., 1979, 240, p. 46-55.
Rahn H., Garey C., Balmas K. - Proc. Natl. Acad. Sci., 1977, 74, p. 3095-
    3098.
Respiratory Function in Birds, Adult and Embryonic / Ed. by J.Piiper.
    Berlin, Heidelberg, New York: Springer, 1978.
Romijn C. - Poultry Sci., 1950, 29, p. 42-51.
Romijn C., Roos J.- J. Physiol. (L.), 1938, 94, p. 365-379.
Schwann T. De necessitate aeris atmospherici ad evolutionem pulli in ovo
    incubito. Dissertation. B., 1834.
Seymour R.S., Rahn H. - In: Respiratory Function in Birds, Adult and
    Embryonic / Ed. by J.Piiper. Berlin, Heidelberg, New York: Springer,
    1978, p. 243-246.
Tazawa H. - In: Respiratory Function in Birds, Adult and Embryonic / Ed. by
    J.Piiper. Berlin, Heidelberg, New York: Springer, 1978, p. 274-291.
Tazawa H. - Am. Zool., 1980, 20, p. 395-404.
Visschedijk A.H.J. - Br. Poultry Sci., 1968, 9, p. 173-184, 185-196, 197-
    210.
Visschedijk A.H.J. - Am. Zool., 1980, 20, p. 469-476.
Vleck C.M., Vleck D., Hoyt D.F. - Am. Zool., 1980, 20, p. 405-416.
Wangensteen O.D. - Respir. Physiol., 1972, 14, p. 64-74.
Wangensteen O.D., Rahn H. - Respir. Physiol., 1970/71, 11, p. 31-45.
Wangensteen D., Weibel F.R.-Respir. Physiol., 1982, 47, p. 1-20.
Wangensteen O.D., Wilson D., Rahn H. - Respir. Physiol., 1970/71, 11, p.16-30.
White F.N., Bartholomew G.A., Kinney J.L. - Physiol. Zool., 1978, 51, p. 140-
    154.

# ADAPTATION OF AVIAN EGGS TO EXTREME ENVIRONMENTS

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## INTRODUCTION

Since birds breed in a remarkable diversity of habitats, their eggs serve
as an excellent tool for identifying key patterns of adaptations to stress-
ful environments. In fact, their utility for studying adaptation extends
into several fields of interest. First, although adult behavior can protect
eggs from certain environmental hazards, particularly thermal extremes
(see Drent, 1975; Carey, 1980a, for review), avian embryos are more exposed
to variation of the physical environment than are those of viviparous ver-
tebrates. Since reproduction is often the most vulnerable aspect of the life
cycle of many organisms and since reproduction must be successful in order
for a species to colonize new habitats, avian eggs provide an interesting
example of adjustment of reproductive modes to environmental stress. Further,
avian eggs are unique in vertebrate reproduction since they exchange gases,
but not solids or liquids (with the possible exception of eggs of a few
species laid in contact with liquid water, Sotherland, 1979 ), with the en-
vironment (Wangensteen and Rahn, 1970-71). Since the gaseous environment varies
in different habitats, avian eggs can be used to determine how gas-exchange
systems have been adjusted to environmental variability. Finally, the avian
eggshell, the barrier between the embryo and its environment, is an excel-
lent example of a biological feature that has evolved in compromise between
mutually antagonistic requirements. The eggshell must be thick enough to
bear the weight of the egg contents and incubating adult, yet thin enough
to be cracked by the hatching chick. And, perhaps most interestingly, the
eggshell must have the appropriate permeability not only to afford adequate
diffusion of oxygen into the shell to support metabolic requirements of the
embryo, but also to restrict excessive losses of $CO_2$ and water vapor from
the egg. Since gas exchange and the qualities of the eggshell which deter-
mine rates of gaseous flux might be predicted to be one of the most sensi-
tive characteristics of avian eggs to environmental variation, the purpose
of this paper is to review current knowledge concerning how the properties
of the avian egg relating to gas exchange vary within species breeding over
geographical gradients or among species breeding in diverse gaseous envi-
ronments.

## ENVIRONMENTAL EFFECTS ON GASEOUS DIFFUSION

As described in detail in the previous papers in this symposium, avian
eggs exchange $O_2$, $CO_2$, and $H_2O$ vapor through common pathways in the eggshell
principally by the process of diffusion (Wangensteen et al., 1970-71; Paga-
nelli et al.,1975; Paganelli  et al., 1978; Paganelli, 1980). We can predict
how the physical environment can influence gaseous diffusion by reviewing
the factors that determine the rate of flux of gas between the environment
and the embryo. Gaseous flux ($\dot{M}$, in $cm^3$ STPD $\cdot$ $sec^{-1}$) is described by a mo-
dification of the Fick equation (Wangensteen et al., 1970-71; Paganelli et
al., 1975):

$$\dot{M} = (D/RT) \cdot (Ap/L) \cdot \Delta P, \tag{1}$$

where $D$ = effective binary diffusion coefficient($cm^2 \cdot sec^{-1}$), $RT$ = gas constant and absolute temperature ($cm^3 STPD \cdot cm^{-3} \cdot torr^{-1}$), $Ap$ = effective pore area ($cm^2$), $L$ = length of the diffusion path, or shell thickness (cm), and $\Delta P$ = partial pressure difference of gas across the shell (torr). This equation points out two aspects of the physical environment that can alter $\dot{M}$, namely $D$ and $\Delta P$.

Since $D$ is a function of barometric pressure ($P_B$) (see below) and since environmental gas tensions comprise part of the $\Delta P$ for each gas, we will find the best examples of adjustments to these environmental features in eggs laid at high altitudes and in diverse gaseous environments, respectively. Before describing the problems posed by variation in $D$ and $\Delta P$ and reviewing the available data on eggs of birds living in these habitats, we must first address the following question: what evidence exists concerning whether variation in $D$ or $\Delta P$ for any gas would actually influence $\dot{M}$ sufficiently that differential mortality would result and select for compensatory modifications in eggshell structure and/or embryonic physiology?

Such little information exists concerning embryonic tolerances of variation in $\dot{M}_{O_2}$, $\dot{M}_{CO_2}$, and $\dot{M}_{H_2O}$ that it is difficult to determine what the actual impact of variation in $D$ or $\Delta P$ would be under certain circumstances. However, considerable information has accumulated concerning normal patterns of gas exchange in numerous species (Rahn, Ar, 1974; Ar, Rahn, 1978; Hoyt, Rahn, 1980; Vleck et al., 1980). Such patterns are strikingly similar despite a 45,000-fold range in egg weight and an 8-fold range in incubation period among all avian eggs (Rahn, Ar, 1974). Eggs just prior to pipping lose an average of 16% of the initial weight of the egg as water vapor during incubation (Ar, Rahn, 1978), the amount of $O_2$ consumed per gram embryo (and presumably the amount of $CO_2$ consumed per gram embryo) varies only slightly (Ar, Rahn, 1978; Hoyt, Rahn, 1980), and the $\Delta P_{O_2}$ and $\Delta P_{CO_2}$ and final levels of $O_2$ and $CO_2$ in the aircell just prior to pipping fall within narrow ranges (Rahn et al., 1974; Hoyt, Rahn, 1980). These data do not indicate that avian embryos are intolerant of wide variation in rates of gas exchange, but that development takes place in a common gaseous environment, despite large differences in egg and hatchling weights and incubation periods. Such similarity is attributed to the intercoordinated evolution of eggshell permeability to gases, determined by $Ap$ and $L$, with the incubation period and egg weight (Ar, Rahn, 1978).

Experimental determination of tolerances of avian embryos to variation in external gas tensions is limited to studies on eggs of domestic fowl (Gallus domesticus). Hatchability severely declines due to hypoxia or hypercarbia in domestic fowl embryos if small portions of the eggshell are blocked just prior to the onset of pulmonary respiration (Visschedijk, 1968; Tazawa et al., 1971). Freeman (1962) observed that mortality was increased from nominal levels to almost 70% if air flow in incubators was increased above recommended levels; he attributed such mortality to increased losses of $CO_2$ but had no evidence to confirm his theory. Hatchability is unusually low in eggs of domestic fowl incubated at $O_2$ concentrations below 15% or above 40% or at concentrations of $CO_2$ above 1% (Lundy, 1969).

Preliminary results from manipulation of eggshell permeability to gases in eggs of red-winged blackbirds (Agelaius phoeniceus) indicate that embryos of wild birds may be fairly tolerant of variation in rates of gas exchange during incubation. Eggshells were treated with waxy coatings to decrease Ap or were punctured over the aircell to increase Ap. While flux of $O_2$, $CO_2$, and $H_2O$ vapor were all affected by such treatment, only rates of water loss were measured. Embryos in naturally incubated eggs were still able to hatch from these eggs despite a 3-fold variation in rates of daily water loss and a final water content ranging from 80-89% (Carey, unpublished data). Further studies are clearly needed to establish tolerance limits of embryos of wild birds to variation in rates of gas exchange.

If we temporarily accept the assumption that variation in D or $\Delta P$ beyond certain limits could cause lethal desiccation or disruption of the acid-base status of the embryo, we can now ask how these features of the environment could modify $\dot{M}$ for any gas and what sorts of solutions may have evolved by avian species to meet these challenges.

EFFECTS OF THE DIFFUSION COEFFICIENT ON GASEOUS EXCHANGE

According to gas laws and theoretical predictions, the effective diffusion coefficient, D, for any gas is inversely proportional to barometric pressure (Reid, Sherwood, 1966; Paganelli et al., 1975). Therefore, gases exchanged between an embryo and its environment should diffuse more rapidly at low $P_B$, all other factors in Eq. 1 held equal, at rates inversely proportional to the decrement in $P_B$ below 760 torr (Paganelli et al., 1975; Paganelli, 1980). Several experiments have verified that eggs of domestic fowl exposed to hypobaria exhibit enhanced rates of loss of $CO_2$ and $H_2O$ vapor and uptake of $O_2$ at value close to predictions based on the increase in D for each gas (see Carey, 1980b, for review).

The problem for an avian embryo laid at high altitude is this: as altitude increases and $P_B$ decreases, the increases in $D_{CO_2}$ and $D_{H_2O}$ will cause progressively greater rates of loss of these two gases. Above certain altitudes, these enhanced rates of loss could cause lethal disruption of acid-base balances and desiccation of the embryo. Concurrently, the $P_{O_2}$ of the ambient air in the ambient air decreases with $P_B$. Although the elevation in $D_{O_2}$ can ameliorate in part the effect of lower $P_{O_2}$ (Visschedijk et al.,1980), the embryo will be unable to obtain sufficient $O_2$ above certain altitudes to meet the demands for normal growth and regulation. Therefore, the avian egg at high altitude is confronted with a classical and striking example of conflicting requirements: restricting losses of $CO_2$ and $H_2O$ vapor from the egg while affording diffusion of adequate levels of $O_2$. How has this problem been solved?

Shell membranes initially pose considerable resistance to diffusion of $O_2$ in the early stages of incubation (Kutchai, Steen, 1971; Lomholt, 1976a; Tullett, Board, 1976). After the shell membranes of eggs of domestic fowl dry, the shell and the outer shell membrane (the "outer barrier") provide about $1/3$ the total resistance to $O_2$ diffusion, the other 2/3 by the "inner barrier" comprised of the inner shell membrane, water layer, and membrane of the chorioallantois (Bissonnette, Metcalfe, 1978; Piiper et al., 1980). No

comparable breakdown of the relative resistances of inner and outer barriers are available for eggs of wild birds.

If maximizing $O_2$ availability to the embryo were the most important goal for optimal hatching success, we might predict that the following characteristics of eggs laid at high altitude would differ from those of eggs of the same species laid in the lowlands: 1) increase in Ap or 2) decrease in L, both or either of which would reduce resistance to diffusion of $O_2$, 3) decrease in parental attentiveness on the nest to result in a greater $\Delta P_{O_2}$ in the nest microenvironment, or 4) decrease in resistance to $O_2$ diffusion in the inner barrier, an increase in the $O_2$ carrying capacity of embryonic blood, an increase in the tolerance of embryonic tissues to hypoxia, or other physiological changes in the embryo. If modifications 1-3 have been completed in the evolution of montane populations, each or all could conceivably result in adequate supplies of $O_2$ but also increase the rate of losses of $CO_2$ and $H_2O$. The only adjustments that would not affect $CO_2$ and $H_2O$ vapor losses but would still promote normal growth and development would be those included in option 4.

If minimizing losses of $CO_2$ and $H_2O$ vapor has proven to be the most essential for maximizing embryonic hatchability at low $P_B$, the following options may have been utilized in the evolution of montane populations: 1) decrease in Ap or 2) increase in L which would increase the resistance to diffusion of these gases, 3) increase adult attentiveness on the nest to reduce $\Delta P_{CO_2}$ and $\Delta P_{H_2O}$,,or 4) increasing the relative water content of fresh eggs and the buffering capacity. This last option would not counteract the increased rates of losses of these gases, but would ensure that the final water content and acid-base status of the pipped embryo would be similar to those found in embryos incubated in the lowlands. If options 1-3 were utilized, we would expect that rates of diffusion of these gases would be independent of $P_B$ in these changes were made in direct proportion to the variation in $P_B$ (see Rahn et al., 1977). However, if option 4 were utilized, we can expect that rates of diffusion of these gases would increase with decreasing $P_B$ but that the final water content of the pipped embryo and its acid-base status would be independent of $P_B$. Finally, we might predict that if options 1-3 were adopted as measures to control rates of losses of $CO_2$ and $H_2O$, the ability to take up adequate $O_2$ for normal requirements would be compromised above certain altitudes.

Approximately 21 species of birds breed between 4300 and 6500 m and many more breed between 3000 and 3000 m (Rahn, 1977). Of these, very few have populations of the same species breeding at sea level, or even more importantly, breeding over an entire altitudinal gradient. Data are now available on eggs of 3 passerine species and 3 groups of Gallus domesticus breeding between sea level and high altitude locations above 3000 m. Since no study has yet investigated the problems of $CO_2$ diffusion at high altitude, we will concentrate our attention on the problems of $O_2$ and $H_2O$ vapor.

The following results indicate that control of $H_2O$ vapor and $CO_2$ diffusion has been more compelling than maximizing $O_2$ uptake, at least to altitudes around 3000 m. Daily rates of water losses do not vary significantly in naturally incubated eggs of red-winged blackbirds (Carey et al., 1983) and white-crowned sparrows (Zonotrichia leucophrys) (Carey, unpubl. data)
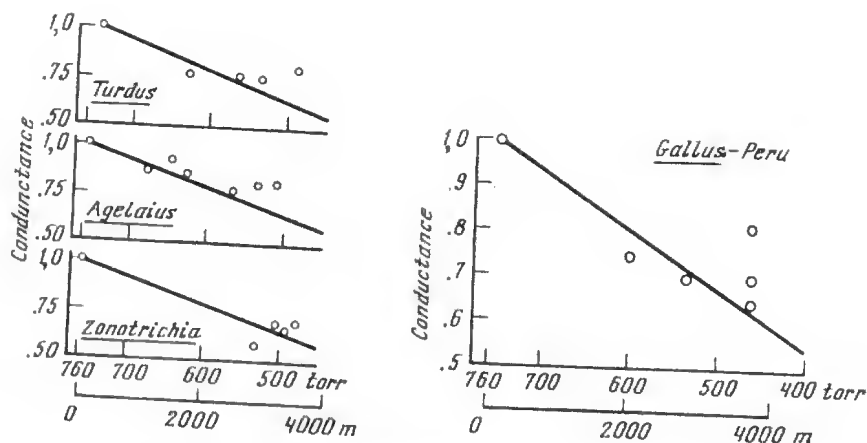
F i g. 1. Relation of relative conductance of eggs to water vapor to $P_B$ (torr) and altitude (m) in three species of passerines. In each case, the actual mean for each population at sea level was standardized at 1.0, and mean values for populations at other altitudes were plotted as a fraction of the sea level value. The line in each drawing represents the reduction expected in conductance if it wsre to be decreased in actual proportion to the decrease in $P_B$ at all altitude locations. Data are modified from Carey et al., 1983, and Carey, unpublished data

F i g. 2. Relation of relative conductance of eggs to water vapor to $P_B$ (torr) and altitude (m) in populations of Gallus domesticus in Peru. The average $G_{H_2O}$ of the sea level population (Lima) was standardized as 1.0 and those of birds living at higher altitudes are plotted as a fraction of the sea level value. The line represents the reduction expected in conductance if it were to be decreased in actual proportion to the decrease in $P_B$ at all altitude locations. Unpublished data were furnished by F. Leon-Velarde, J.Whittembury, C.Carey, H.Rahn, and C.Monge

breeding between sea level and 3050 and 3660 m, respectively. These rates are independent of $P_B$ despite an increase in $D_{H_2O}$ at the highest locations of 31 and 36% for red-winged blackbirds and white-crowned sparrows, respectively. Further, the final water content of pipped red-winged blackbird embryos were independent of $P_B$ over a 2900 m altitudinal gradient (Carey et al.,1983).

The independence of rates of $H_2O$ vapor diffusion from variation in $P_B$ appears to have been achieved by 3 passerine species (red-winged blackbirds, white-crowned sparrows, and American robins, Turdus migratorius) by a reduction in Ap. This conclusion is based on measursments of eggshell conductance to water vapor ($G_{H_2O}$), eggshell thickness, fresh water content of eggs, and nest attentiveness of adults in populations of thess species ranging from near sea level to over 3000 m. Of these characteristics, the only significant factor correlated with $P_B$ was $G_{H_2O}$ (Carey st al., 1983; Carey, unpubl data). Since Ap cannot be measured directly, $G_{H_2O}$ is measured by the method of Ar et al (1974). Since $G_{H_2O}$ is a function of both Ap and L and since. L doss not vary significantly with $P_B$ in these species, the change in $G_{H_2O}$ can be attri-

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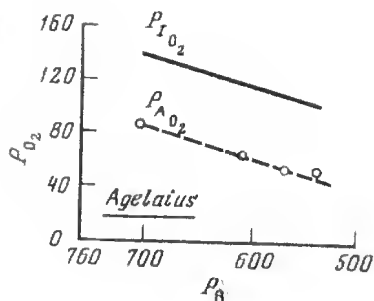
F i g. 3. Comparison of decrease of the ambient oxygen tension ($P_{I_{O_2}}$ in torr) to calculated values of air cell $O_2$ tensions ($P_{A_{O_2}}$ in torr) in eggs of red-winged blackbirds laid at 4 locations. Data are modified from Carey et al., 1982

buted to a reduction in Ap. A similar reduction in $G_{H_2O}$ has been described in eggs laid in montane locations in 3 groups of domesticated fowl (Wangensteen et al., 1974; Rahn et al., 1977; F.Leon-Velarde et al.,unpubl. data).

$G_{H_2O}$ decreases in approximate proportion to the decrease in $P_B$ in these three species of passerines to about 2400-2900 m, then begins to increase slightly (Fig. 1). A similar relation of $G_{H_2O}$ to $P_B$ is found in eggs of chickens collected in Peru from sea level (Lima) to about 3900 m (Puno) (Fig. 2). The average $G_{H_2O}$ of three groups of eggs at the highest location in Peru average 64, 75 and 83% of the sea level value; though the $P_B$ at that location is reduced to 62 of 760 torr (F.Leon-Velarde et al., unpubl. data). Fewer collecting sites have been used in two other studies on chickens, but a similar undercompensation for the decrease in $P_B$ above 3000 m is observed (see Carey, 1980b). Chickens raised at 3500 m in the Himalayas for about 40 years (Rahn, 1977) produced eggs with an average $G_{H_2O}$ that was 72% of the average value of eggs laid at sea level; the $P_B$ at the montane site was 69% of the sea level value (Rahn et al., 1977). Mean $G_{H_2O}$ of eggs of chickens maintained for at least 15 years at 3800 m in California was 68% of the value of lowland eggs; the $P_B$ at this location was 63% of that at the collection site near sea level (Wangensteen et al., 1974).

A possible explanation for the increase in $G_{H_2O}$ at the higher altitudes above 2400-3000 m might be that a slight increase in Ap may provide some improvement in $O_2$ diffusion, especially for the population of chickens at 3900 m in Peru (Fig. 2). Oxygen consumption has only been measured in one species over an altitudinal gradient: (Fig. 3) metabolic rates appear independent of $P_B$ from 200 to 2900 m in eggs of red-winged blackbirds, despite a decrease in the calculated air cell oxygen tension ($P_{A_{O_2}}$) to about 60 torr, a value about 60% of the $P_{A_{O_2}}$ measured in other bird eggs at sea level (Rahn et al., 1974). Oxygen consumption of chickens maintained at 3800 m was significantly decreased below sea level values (Wangensteen et al., 1974), but this may reflect the overall lack of ability of domesticated strains to function in even mild hypoxia between 1700 and 3800 m (Wangensteen et al., 1974; Rahn, 1977; Visschedijk et al., 1980). Although measurements of $O_2$ consumption are not available for embryos of other wild birds at high altitude, we may conclude, on the basis that hatchling weight and incubation period do not vary with altitude, that oxygen consumption probably remains normal in embryos of white-crowned sparrows and horned larks (Eremophila alpestris)

to 3475 and 3600 m, respectively (Carey et al., 1982). This achievement in such hypoxic circumstances may in part be due to a slight increase in Ap, but certainly must also involve other changes in the inner barrier and in the physiological characteristics of the embryos (Carey et al., 1982).

The colclusion supported by existing evidence on these 6 groups of birds is that the conservation of $H_2O$ and/or $CO_2$ is the most important aspect of adaptation to low $P_B$, at least to around 3000 m. The independence of rates of $H_2O$ loss from variation in $P_B$ has apparently involved a reduction in Ap in approximate proportion to the reduction in $P_B$. Above approximately 3000 m, Ap may increase slightly and could facilitate $O_2$ diffusion, though alterations in the physiological properties of the embryo could certainly also be employed to maximize $O_2$ availability in such hypoxic environments. Therefore, the solution to the mutually conflicting requirements of maximizing $O_2$ uptake and minimizing $CO_2$ and $H_2O$ losses may be solved differently at varying altitudes.


## EFFECTS OF $\triangle$P ON GASEOUS EXCHANGE

Certain avian species lay eggs in gaseous environments, such as cavities, burrows, floating nests saturated with water, or underground. These environments differ substantially from the gaseous conditions in which most birds nest. Since $\dot{M}$ depends in part of the $\triangle$P for any gas, it is of interest to determine how eggs of these species differ, if at all, from those of other birds. In these instances, we are not able to compare eggs of the same species laid in both "normal" aerial environments and diverse ones; we are limited to comparisons of values with those predicted on the basis of allometric equations (Ar, Rahn, 1978).

Underground nests .- Probably the most interesting modification of the eggshell permeability to gaseous diffusion has been described in eggs of species laying in nests buried under soil or rotting vegetation (Seymour, Rahn, 1978; Seymour, Acherman, 1980). Since this general topic will be covered in great detail in another paper in this symposium, only the following point needs to be emphasized. As Seymour and Acherman (1980) points out, such nests are almost, if not fully, saturated with water vapor. Therefore, the importance of the eggshell porosity in regulating rates of water exchange during incubation becomes decreased. The Ap of eggs laid by these species has been enlarged relative to predicted values, probably to ensure adequate exchanges of $O_2$ and $CO_2$ in highly hypoxic and hypercarbic environments.

Burrows - Certain species nest in burrows in sand or soil. Due to the lack of appropriate ventilation, gas tensions may become quite hypoxic and hypercarbic; in addition, most are fully saturated with water vapor. For instance, concentrations of $O_2$ and $CO_2$ may reach 15.1% $O_2$ and 6.5% $CO_2$ in burrows of the bee-eater (Merops apiaster) during the nestling period (White et al., 1978). The most complete study on eggs of a species burrowing in such conditions has been done on bank swallows (Riparia riparia). Burrows averaging 0.56 cm (Birchard, Kilgore, 1980) may contain gaseous concentrations reaching 3% $CO_2$ and 17% $O_2$(Birchard, Kilgore, 1980; Wickler, Marsh,1980). The $G_{H_2O}$ of cliff swallow eggs is significantly larger than those of a close

relative, barn swallows (<u>Hirundo rustica</u>) (Birchard, Kilgore, 1980). Such enlargement of $G_{H_2O}$ may increase rates of $O_2$ and $CO_2$ exchange.

Surprisingly, some species nesting in burrows do not lay eggs that exhibit significantly larger $G_{H_2O}$. Some seabirds of the family Procellariformes, nest in burrows which may vary in length, in the case of the Bonin petrel (<u>Pterodroma hypoleuca hypoleuca</u>), from 0.6 to 3 m (Pettit et al., 1983). Despite fully saturated nest interiors, $G_{H_2O}$ is significantly reduced in these species, often to 50% of the predicted level (see summary by Whittow, 1980).The reduction in eggshell permeability is interpreted to be a adaptation to prolonged incubation periods (Grant et al., 1982).

<u>Wet nests</u> - Eggs of birds laid in nests that float on water and which are often fully saturated with liquid water may exhibit significantly larger values of $G_{H_2O}$ than predicted on the basis of egg weight (Ar, Rahn, 1978). This adjustment presumably counteracts the problems posed by uptake of liquid water (Sotherland, 1979) and/or a low $\Delta P_{H_2O}$ and allows fractional water loss during incubation to approximate the average levels of other species (Lomholt, 1976b). In conclusion, considerable variety in eggshell permeability is found in birds nesting in diverse gaseous environments. So few studies have been done on these species that it is difficult to make generalizations at this point. Hopefully, future studies will be directed toward the goal of determining what selective pressures have acted on these species to select for the observed differences in eggshell characteristics.

SUMMARY

This paper has reviewed only one aspect of adaptation of avian eggs to extreme environments, namely adjustments of the eggshell structure that affect exchange of gases between the embryo and the environment. Certainly, birds breed in other kinds of environments that provide serious challenges to reproduction than those detailed here, but adult behavior compensates for many of these problems (see Carey, 1980a for review). Therefore, this paper reflects what is currently known about adaptation of the egg, rather than adult behavior, to environmental stress. Hopefully, further research on species breeding in diverse environments will provide more evidence of the variety of adaptations in this reproductive mode.

ACKNOWLEDGEMENTS

References

Ar A., Rahn H. - In: Respiratory Function in Birds, Adult and Embryonic. B.: Springer-Verlag, 1978, p. 227-236.

Birchard G.F., Kilgore D. - Physiol. Zool., 1980, 53, p. 284-292.

Bissonnette J.M., Metcalfe J. - Resp. Physiol., 1978, 34, p. 209-218.

Carey C. - BioScience, 1980a, 30, p. 819-823.

Carey C. - Am. Zool., 1980b, 20, p. 449-459.

Carey C., Garber S.D., Thompson E.L., James F.C. - Physiol. Zool., 1983.

Carey C., Thompson E.L., Vleck C.M., James F.C. - Auk, 1982.

Drent R.H. - In: Avian Biology, Vol. B. N.Y.: Academic Press, 1975, p. 333-420.

Grant G.S., Pettit T.N., Rahn H. et al. - Auk, 1982, 99, p. 236-242.

Hoyt D.F., Rahn H. - Resp. Physiol., 1980, 39, p. 255-264.

Kutchai H., Steen J.B. - Resp. Physiol., 1971, 11, p. 265-278.

Lomholt J.P. - J. Exp. Zool., 1976a, 198, p. 177-184.

Lomholt J.P. - J. Comp. Physiol., 1976b, 105, p. 189-196.

Lundy H.L. - In: The fertility and hatchability of the hen's egg. L.: Eberhard, Olwen and Boyd, 1969, p. 143-176.

Paganelli C.V. - Am. Zool., 1980, 20, p. 329-338.

Paganelli C.V., Ackerman R.A., Rahn H. - In: Respiratory function in birds, adult and embryonic. B.: Springer-Verlag, 1978, p. 212-218.

Paganelli C.V., Ar A., Rahn H., Wangensteen O.D. - Resp. Physiol., 1975, 25, p. 247-258.

Pettit T.N., Grant G.S., Whittow G.C. et al. - Am. J. Physiol., 1982, 11, p. R121-R128.

Piiper J., Tazawa H., Ar A., Rahn H. - Resp. Physiol., 1980, 39, p. 273-284.

Rahn H. - In: Respiratory adaptations, capillary exchange, and reflex mechanisms. Delhi, Vallabhbhai Patel Chest Institute, 1977, p. 94-105.

Rahn H., Ar A. - Condor, 1974, 76, p. 147-152.

Rahn H., Carey C., Balmas K. et al. - Proc. Natl. Acad. Sci. USA, 1977, 74, p. 3095-3098.

Rahn H., Paganelli C.V., Ar A. - Resp. Physiol., 1974, 22, p. 297-309.

Reid R.C., Sherwwod T.K. Properties of gases and liquids. N.Y.: McGraw-Hill, 1966.

Seymour R.S., Ackerman R.A. - Am. Zool., 1980, 20, p. 437-447.

Seymour R.S., Rahn H. - In: Respiratory Function in birds, adult and embryonic. B.: Springer-Verlag, 1978, p. 243-246.

Tazawa H., Mikami T., Yoshimoto C. - Resp. Physiol., 1971, 13, p. 352-360.

Tullett S.G., Board R.G. - Brit. Poult Sci., 1976, 17, p. 441-450.

Visschedijk A.H.J. - Brit. Poult. Sci., 1968, 9, p. 173-184.

Visschedijk A.H.J., Ar A., Rahn H., Piiper J. - Resp. Physiol., 1980, 39, p. 33-44.

Vleck C.M., Vleck D., Hoyt D. - Am. Zool., 1980, 20, p. 405-416.

Wangensteen O.D., Rahn H. - Resp. Physiol., 1970/71, 11, p. 31-45.

Wangensteen O.D., Rahn H., Burton R.R., Smith A.H. - Resp. Physiol., 1974, 21, p. 61-70.

Wangensteen O.D., Wilson D., Rahn H. - Resp. Physiol., 1970/71, 11, p. 16-30.

White F.N., Bartholomew G.A., Kinney J.L. - Physiol. Zool., 1978, 51, p. 140-154.

Wickler S., Marsh R.L. - Physiol. Zool., 1980, 53, p. 435-462.

# PHYSIOLOGY OF MEGAPODE EGGS AND INCUBATION MOUNDS

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## INTRODUCTION

The incubation biology of birds in the family Megapodiidae is unique be-
cause the eggs are laid underground or in mounds of earth and decomposing
vegetation where heat comes from solar, geothermal or microbial sources,
rather than from a parent (Frith, 1956a). This method of incubation is cor-
related with an interacting set of physiological and behavioral adaptations
of the embryos and hatchlings that further distinguishes the family from all
other birds. This report concerns selected aspects of the incubation physio-
logy of Brush Turkeys, Alectura lathami, and Mallee Fowl, Leipoa ocellata
which were studied near Renmark and on Kangaroo Island in South Australia.
The investigations have been directed toward an understanding of the condit-
ions inside the incubation mounds and the respiratory and metabolic adaptati-
ons of the embryos to the mound environment.

## THE MOUND ENVIRONMENT
### Microbial Respiration

Megapode mounds are heated by a heterogeneous assemblage of microorga-
nisms, chiefly thermophilic fungi, that develops in the litter collected by
the birds. Although the process involving heat production often is termed
fermentation, in fact it is respiration and wholly dependent of $O_2$ in the
mound. No part of the mound is anaerobic (Fig. 1) and the microorganisms do
not produce significant $CO_2$ in the absence of $O_2$. In the Brush Turkey mound,
there is a correlation between temperature and gas tensions which show that
both heat and gas move by diffusion through the mound material. Furthermore,
there is a close relationship between $P_{O_2}$ and $P_{CO_2}$ at any point in the mound
(Fig. 2). The slope of the data is close to the line predicted in a system
where gas moves by diffusion alone and where the respiratory exchange ratio
(RE) is 0.75, the value measured in individual samples of mound material.
If convection were important, the slope of the line would be less because
the difference in diffusion rates of $CO_2$ and $O_2$ is obscured by bulk movement
of gas. The data also deny the importance of fermentation because it would
tend to increase RE above 1.0. A RE of 0.75 indicates that the microorganisms
either decompose a large proportion of lipids and proteins or they break
down carbohydrates incompletely into organic acids and other large molecules.

### Mound Thermoregulation

The classical studies of Frith (1956b, 1959, 1962) demonstrated that the
temperature at egg level in Mallee Fowl mounds is regulated within a range
of 32-35°C primarily by the male bird which opens and closes the mound to
control heat transfer. This task involves balancing two heat sources, micro-
bial respiration and solar radiation.

In Brush Turkey mounds, constructed in shade, respiration is the primary
source of heat. During the three to four month period when eggs are present
on Kangaroo Island, core mound temperature is maintained at about 30-34°C.

$P_{O_2}$  $P_{CO_2}$

156  0
144  15
133  24
131  24
130  23
132  23
133  21
133  21
134  23

- 150
- 100
- 50
cm
Ground level
0

20
25
30
35
30
25
25

0    50    100    150    200    250 cm
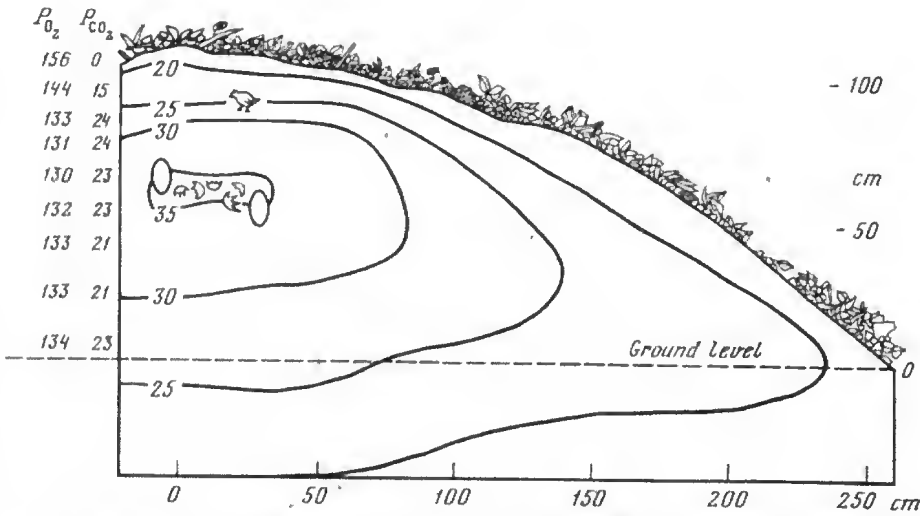
F i g. 1. Section through an active Brush Turkey mound showing temperature isotherms throughout and gas tensions in the center only. The positions of eggs and a hatched chick, discovered when the mound was excavated, are indicated

There is little doubt that the mound temperature is also regulated by the male Brush Turkey, but the physiological characteristics of the mound itself are important in temperature stability. First, with a mass of 2-4 metric tonnes, the mound has a great thermal inertia and is independent of daily temperature changes around it. Second, the relationship between heat production and heat loss is such that the mound tends to stabilize at what is termed the equilibrium temperature when heat production equals loss. To illustrate the principles of this concept it is useful to refer to a simple spherical model of the mound which shows how equilibrium temperature is affected by factors such as mound size, ambient temperature, thermal conductivity and heat production (Fig. 3).

Heat loss from the mound is related to the difference between mound and ambient temperature (Fig. 3A). Warmer ambient temperatures reduce the rate of heat loss and the line shifts in parallel to the right. Heat loss is also reduced if the mound is made larger or the thermal conductivity decreases; in this case a rotational shift occurs (Fig. 3B).

Heat production depends primarily on the age, water content, and temperature of the mound material. Like most biochemical reactions, mound respiration depends on temperature in an exponential fashion at temperatures below 50°C (Fig. 4). Heat produced in the mound tends to increase temperature which in turn increases the rate of heat production. In a large mound made of fresh litter, this effect leads to an ever-rising temperature which is limited only by thermal inhibition of respiration at temperatures in the region of 50-70°C. As the mound material ages or dries, the position of the curve shifts downward. Adding fresh litter or wetting the mound increases heat production and lifts the line.
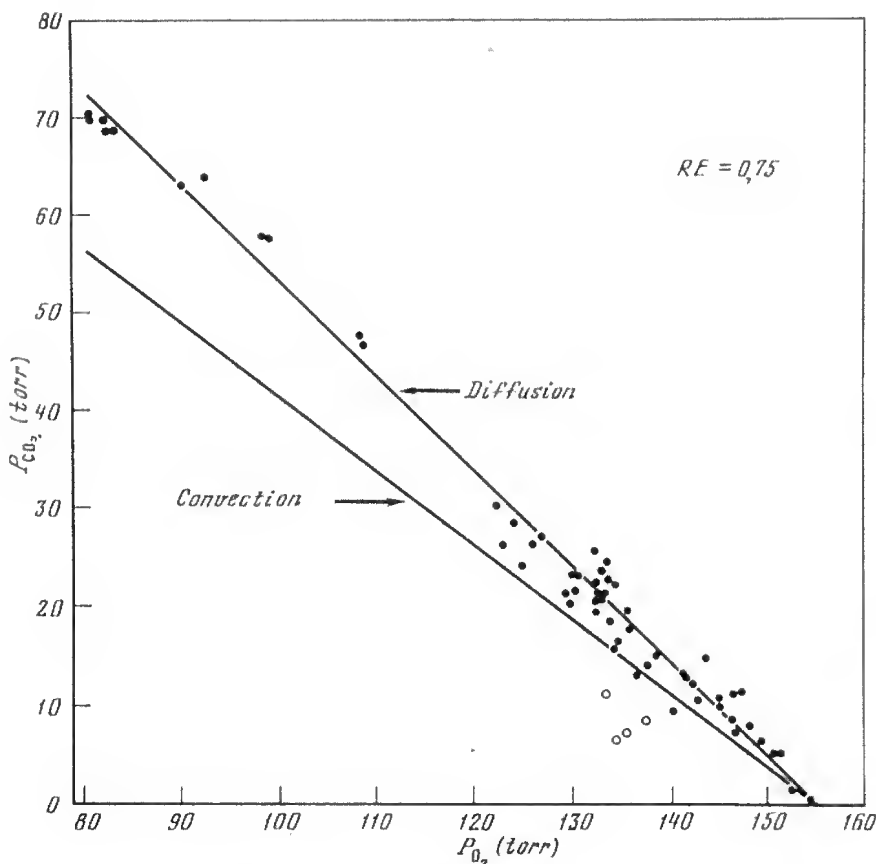
F i g. 2. The relationship between $P_{CO_2}$ and $P_{O_2}$ at various depths in several Brush Turkey mounds. The upper line represents theoretical gas movement through the mound by diffusion only, given a respiratory exchange ratio (RE) of 0.75. The lower line represents gas movement by convection only

When heat production equals heat loss, the mound temperature is constant. This equilibrium temperature can be found at the intersection of the lines for heat production and loss (Fig. 3D). If the mound is cooled, for example by excavations of the bird, the drop in temperature causes heat production to exceed heat loss and the mound rewarms toward equilibrium. On the other hand, if the mound in some way becomes warmer than equilibrium, greater heat loss cools the mound until equilibrium is reached. In this way the mound temperature always tends to move toward the equilibrium point.

Although somewhat of a homeotherm, the mound is incapable of regulating its temperature at a fixed value appropriate for incubation. The bird must measure temperature from time to time and make appropriate adjustments in the mound. To raise the temperature, he simply adds a little fresh litter which has two effects. First, it increases mound size and reduces heat loss. Second, it adds fresh substrates for the microorganisms and increases heat production. These effects combine to shift the equilibrium temperature upward. The acute angle of intersection of the lines for heat production and

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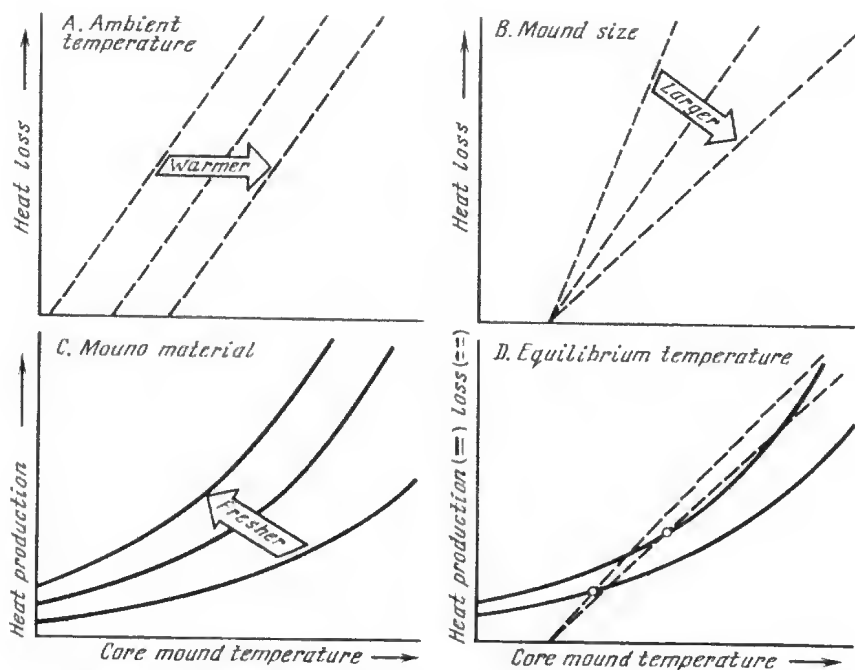
F i g. 3. Models of heat production and heat loss from a spherical mound.
(A) Effect of ambient temperature change on heat loss. (B) Effect of chan-
ges in mound radius on heat loss. Decreased thermal conductivity of the
mound material also reduces heat loss. (C) Effect of age or water content
on heat production. (D) Equilibrium temperature at the intersection of cur-
ves for heat production and loss. Changes in curve positions shift the
equilibrium temperature

heat loss (Fig. 3D) means that only a small layer of litter (e.g. less than
5 cm) needs to be added to greatly affect core mound temperature. With em-
pirical values of respiration rates, thermal conductivity and mound radius,
our model demonstrates that equilibrium temperatures in fact exist; that is,
the curves for heat production and loss intersect in the range of natural
incubation temperatures.

We do not know how often mound temperature is checked and adjusted. Becau-
se temperature and respiration rates change slowly, the intervals between egg
laying are short enough to allow adequate regulation. The stability of mound
temperature was clearly demonstrated by a particular mound we found on Kanga-
roo Island that remained at 35.5°C in the center despite being abandoned by
the bird for at least 6 months through the winter.

Because heat production is related to mound volume and heat loss is re-
lated to surface area, there is a certain mound size, or critical mass, re-
quired for the mound to warm up. This was shown naturally when a Brush Tur-
key constructed, and then abandoned, a small mound about 0.5 m high and
1.5 m in diameter. This mound failed to warm in the first year of its exist-
ence but in the second year, when more material was added to increase the
height to 1.0 m and the diameter to 3.6 m, it warmed and eggs were laid. We
constructed artificial mounds of different sizes and discovered that a mound
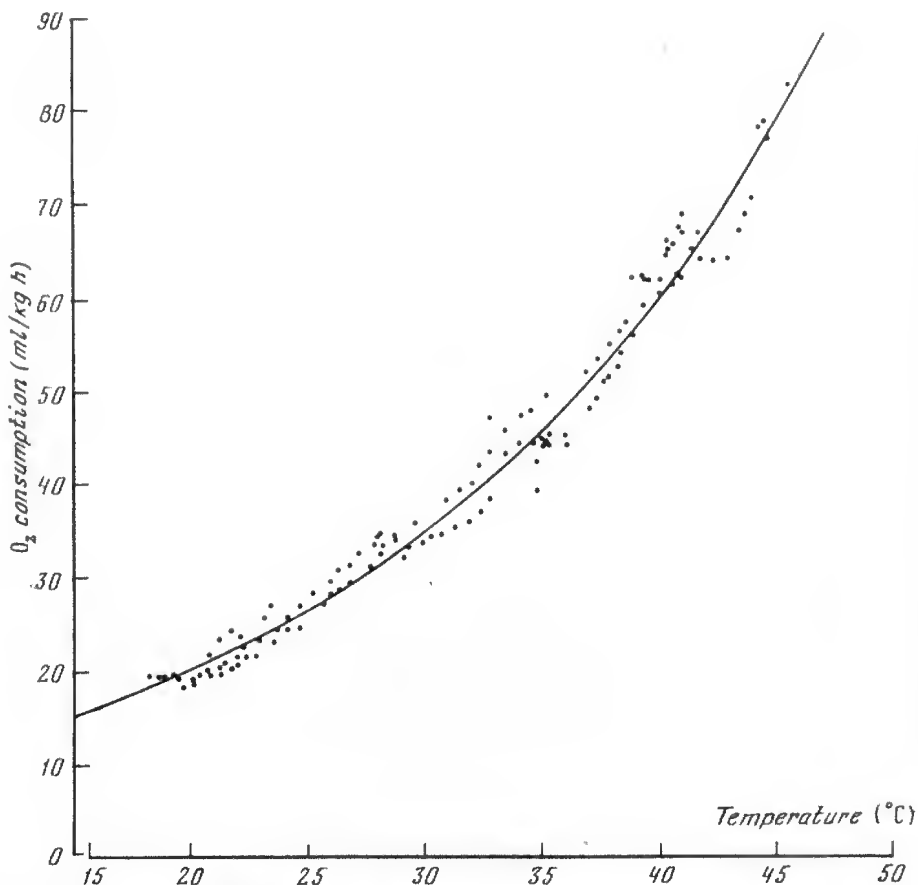
F i g. 4. Effect of temperature on microbial respiration in a sample of Brush Turkey mound material

will not warm to incubation temperature unless it is larger than about 0.75 m high and about 2.0 m in diameter. The average Brush Turkey mound on Kangaroo Island is 1.3 m high and 5.3 m in diameter.

Surface-volume considerations are only partly responsible for the large size of Brush Turkey mounds. If a new mound is not built, enough fresh litter must be incorporated into an old one each year to satisfy the energy requirements of the microorganisms. Thus the older the mound, the larger it becomes. Brush Turkeys often build new mounds, but Australian Scrub Fowl (Megapodius reinwardt) continually add new material to old mounds which grow through the years and can exceed 4 m in height and 20 m in diameter (Frith, 1956a; Crome, Brown, 1979).

Water content of the litter greatly affects the mound thermodynamics. Sufficient moisture is required for microbial respiration, but excess water in the mound can be detrimental. As the mound material becomes wetter, its thermal conductivity increases and the mound loses heat faster. Although this is offset by higher heat production, the litter decomposes more quickly and the Brush Turkey must gather more litter to keep the mound warm during the incubation season.

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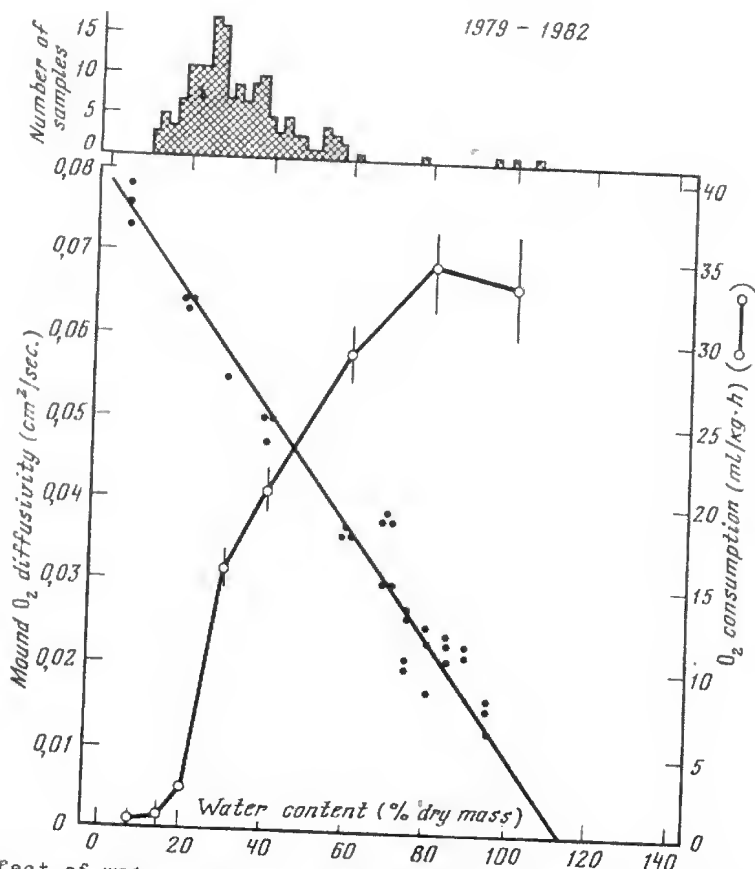
F i g. 5. Effect of water content on microbial respiration and gas diffusivity of the material in a Brush Turkey mound. The histogram shows the water content of a number of samples of material from natural mounds on Kangaroo Island

Mound water also has a profound effect on the gas tensions near the eggs. Added water not only increases respiration by the microorganisms but it also decreases the gas diffusivity by blocking the gas channels between the particles of litter (Fig. 5). Although a wet mound may have an appropriate incubation temperature, the $O_2$ and $CO_2$ tensions may become lethal to the embryos. Therefore the optimal water content is one which allows adequate incubation temperatures without excessive restriction of gas diffusion. It is perhaps significant that natural Brush Turkey mounds on Kangaroo Island are relatively low in water content (Fig. 5). The low heat production conserves substrates while the high gas diffusivity maintains equitable gas tensions. It has been suggested by Frith (1956a, 1962) and Fleay (1937) that the birds may control mound water content by changing mound shape during rain storms.

RESPIRATORY ADAPTATIONS OF THE EMBRYOS

Gas Exchange Across the Shell

Gas exchange in avian eggs occurs by diffusion of $O_2$, $CO_2$ and water vapor through pores in the shell, a process that depends on the conductance of the

859

pores and the difference in gas tension across the shell (Paganelli, 1980).
Birds that nest above ground expose their eggs to gas tensions not greatly
different from those prevailing in the free atmosphere (Walsberg, 1980). In
such uniform conditions, natural selection has produced shell conductances
that are often predictable from egg mass and incubation time (Ar, Rahn, 1978).
There appears to be a selective pressure to produce shell conductances that
lead to an evaporative water loss equivalent to about 15% of the initial egg
weight during incubation (Ar, Rahn, 1980). This water loss creates the "air
cell" between the shell membranes in which the late embryo breathes before
hatching. Too little water loss and the embryo risks drowning by inhaling
fluid in an inadequate air cell but too much water loss exposes the embryo
to dehydration stress. Within the range of tolerable water vapor conductance,
however, shell conductance must be moderated by the requirement for adequate
exchange of $O_2$ and $CO_2$.

High humidity in megapode mounds eliminates the danger of excess dehydrat-
ion but the $O_2$ and $CO_2$ tensions tend to restrict embryonic gas exchange. Me-
gapode eggs are adapted to the mound environment by possessing shells of
high conductance. This is achieved by a thin shell rather than one of high
pore area. For example, the conductance of Brush Turkey shells is more than
twice the value predicted from normal birds, the shell being only half the
predicted thickness but of normal pore area (Seymour, Rahn, 1978). High shell
conductance reduces the $P_{O_2}$ and $P_{CO_2}$ differences across the shell, thereby
compensating for the abnormal mound atmosphere. In the field, the gas tensions
inside the shell of Brush Turkeys ($P_{O_2}$ = 107 torr, $P_{CO_2}$ = 48 torr) are nearly
identical to those found inside most bird eggs ($P_{O_2}$ = 100 torr, $P_{CO_2}$ = 40
torr; Hoyt and Rahn, 1980). In zoos, however, the atmosphere in Brush Turkey
mounds can cause the $P_{O_2}$ to drop to about 65 torr and the $P_{CO_2}$ to rise above
90 torr inside the eggs and this may be the cause of low hatchability in zoos
(Baltin, 1969; Seymour, Rahn, 1978; Seymour, Ackerman, 1980). Potentially se-
vere gas tensions point to the need to provide adequate gas diffusion through
the mound. It has been suggested that the Brush Turkey may dig ventilation
tunnels in the mound if gas tensions become extreme (Baltin, 1969; Seymour,
Ackerman, 1980).

Oxygen consumption by Mallee Fowl and Brush Turkey embryos depends on am-
bient $O_2$ tension in short-term experiments on eggs of all ages (Fig. 6). This
is not unusual as it also occurs in chickens (Visschedijk, 1980). Although
short-term variations in mound $P_{O_2}$ obviously affect egg respiration, particu-
larly near hatching, it is not known whether the prevailing hypoxia in the
mound affects the incubation time or the rates of respiration and growth in
the long-term. The development of the chorioallantois and the increase in its
diffusion capacity closely parallel the gas exchange requirements in chicken
embryos (Fitze-Gschwind, 1973; Piiper et al., 1980; Tazawa, 1980), so it is
possible that the gas exchange capacity of the megapode chorioallantois com-
pensates for the mound environment adjacent to the eggs.

### The Air Cell and Quick Hatching

Despite the high shell conductance and a vapor pressure difference across
the shell due to embryonic heat production, the eggs lose little water because
of high mound humidity. Brush Turkey eggs lose less than 8% of the initial egg
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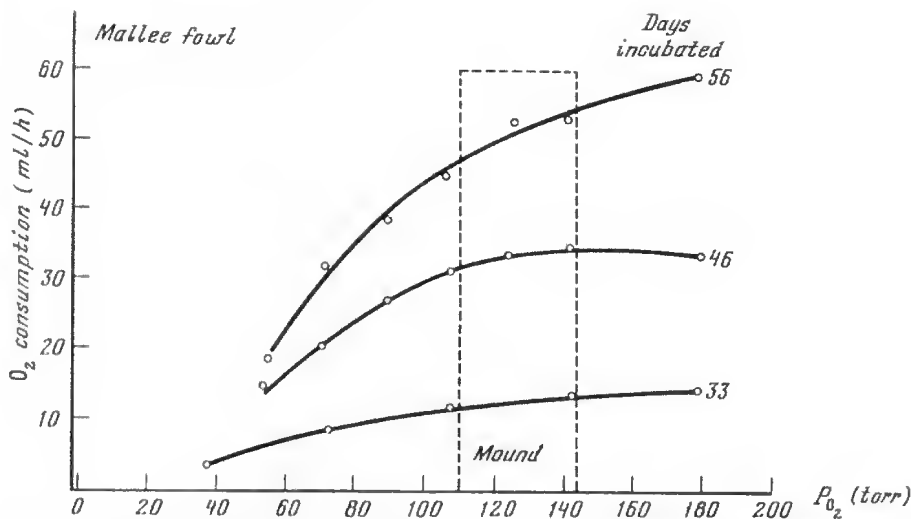
F i g. 6. Short-term effects of ambient $P_{O_2}$ on $O_2$ consumption by Mallee Fowl embryos of different ages. The range of natural mound $P_{O_2}$ is represented by the bar

mass in natural mounds and no useful air cell forms. In most birds, the chick pips internally into the fixed air cell and begins breathing long before the shell is broken; this begins a rather slow transition from chorioallantoic to pulmonary gas exchange (Visschedijk, 1968). Internal pipping is impossible in megapodes because the air space is usually too small and, in any case, it is not fixed in position. Thus the hatching cannot initiate pulmonary respiration until after it breaks through the shell with its feet and the fluid drains from around the head. It is valuable for this process to be quick because the first rupture of the shell membranes disrupts chorioallantoic circulation which provides all gas exchange at the time. When observed in the laboratory, hatching megapodes break through the shell and begin breathing immediately (Baltin, 1969). Blood loss from the chorioallantois indicates that it is perfused until ruptured but circulation stops in less than 2 minutes.

Quick hatching is facilitated by unusually thin shells and strong legs in megapodes. It is not fortuitous that the requirement for high shell conductance is met by relatively thin shells rather than by increased pore area. Protected by the mound, the eggs are in less danger of breaking than are eggs incubated in a nest under a parent. Moreover a thin shell is less expensive for the female to synthesize.

Precocity of Hatchlings

Because megapodes have lost the close association between the eggs and the parents, and the chicks hatch over a period of months at times that are apparently unpredictable, it is understandable that there is absolutely no parental care for the hatchlings (Nice, 1962). Furthermore the chicks hatch about 50 cm below the surface of the mound and they must be strong enough to emerge unassisted. This can require several hours in Mallee Fowl and over a day in Brush Turkeys (Frith, 1959; Baltin, 1969). These problems of early life have selected for hatchlings that are among the most precocial of all

birds (Nice, 1962). They hatch with well developed primary feathers and can fly within the first day (Frith, 1959; Baltin, 1969). They can also thermoregulate successfully within a range of ambient temperatures of at least 5-45°C (D.Booth, unpublished).

Our studies of megapode incubation show a uniform pattern of energy and water utilization that is consistent with the production of highly precocial chicks. First, the incubation periods of Mallee Fowl (62 days; Frith, 1959) and Brush Turkeys (49 days; Baltin, 1969) are respectively 71% and 34% higher than predicted from normal eggs of the same mass (Ar, Rahn, 1978). Although the initial rate of development is slow, megapodes undergo a maturation equivalent to several weeks of post-hatching growth in other galliform birds (Clark, 1964). Extreme precocity is also reflected in the energy utilization during incubation. Mallee Fowl and Brush Turkeys respectively use 94% and 47% more energy during incubation than predicted by eggs of other precocial species (Vleck et al., 1980). The high energy demands of megapode embryos are met by large yolks. Megapodius freycinet eggs are reported to be 67% yolk (Meyer, 1930). Mallee Fowl and Brush Turkey eggs are about 50% yolk. The total lipid content in these eggs is 30-50% higher, and the total energy content is about 25% higher, than the means for other precocial species (Carey et al., 1980). The excessive lipid is balanced by a low initial water content. As we have seen, evaporative water loss is not a problem and the eggs in fact lose copious water during hatching. Carey et al. (1980) have shown that the percentage water content of fresh eggs decreases from a mean of 84.3% in altricial species to 74.7% in precocial species. Megapode eggs carry this relationship farther, being only 66.5% (Mallee Fowl) to 68.4% (Brush Turkey) water. As in other birds (Ar, Rahn, 1980), the percentage water content of the fresh egg is nearly identical with that of the hatching chick.
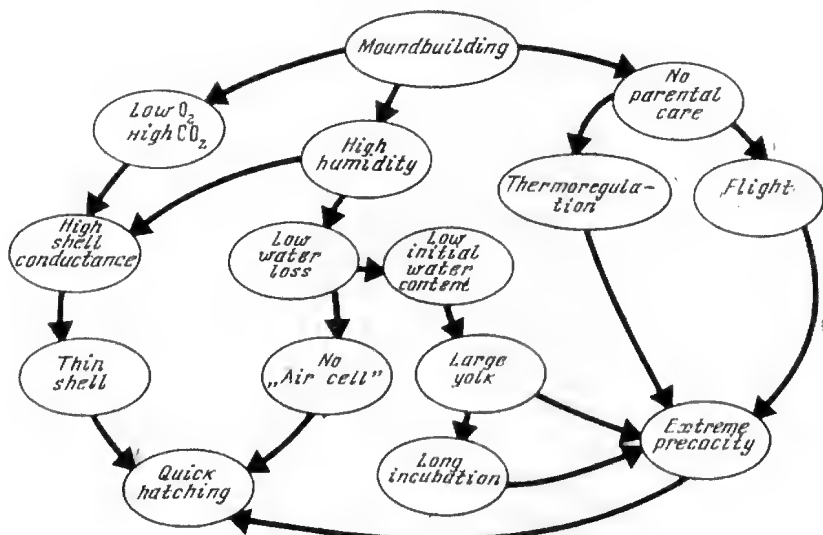


F i g. 7. Interrelations of moundbuilding behavior and the adaptations of megapode eggs and hatchlings

SUMMARY

The physiology of megapode eggs is considered to be continuous with, and adapted to, the physiology of the incubation mound (Fig. 7). With help from the adult, the mound offers protection and stable incubation temperature but subjects the eggs to an unusual gaseous environment. The eggs are adapted to high humidity, low $P_{O_2}$ and high $P_{CO_2}$ by possessing a thin shell which facilitates exchange of respiratory gases and allows quick hatching by the chick which cannot breathe inside the egg. Moundbuilding behavior precludes parental care and selects for large, precocial chicks capable of thermoregulation and flight. This requires long incubation and large energy stores in the egg.

R e f e r e n c e s

Ar A., Rahn H. - In: Respiratory Function in Birds, Adult and Embryonic / Ed. by J.Piiper. Berlin, Heidelberg, New York: Springer-Verlag, 1978, p. 227-236.

Ar A., Rahn H. - Amer. Zool., 1980, 20, p. 373-384.

Baltin S. - Z. Tierpsychol., 1969, 26, p. 524-572.

Carey C., Rahn H., Parisi P. - Condor, 1980, 82, p. 335-343.

Clark G.A. Jr. - Living Bird, 1964, 3, p. 149-167.

Crome F.H.J., Brown H.E. - Emu, 1979, 79, p. 111-119.

Fitze-Gschwind V. - Ergebn. Anat. Entwickl.-Gesch., 1973, 47(1), p. 7-52.

Fleay D.H. - Emu, 1937, 37, p. 153-163.

Frith H.J. - Ibis, 1956a, 98, p. 620-640.

Frith H.J. - CSIRO Wildl. Res., 1956b, 1, p. 79-95.

Frith H.J. - CSIRO Wildl. Res., 1959, 4, p. 31-60.

Frith H.J. The Mallee Fowl. Sydney: Angus and Robertson, 1962.

Hoyt D.F., Rahn H. - Respir. Physiol., 1980, 39, p. 255-264.

Meyer O. - Ornith. Monatsber., 1930, 38, p. 1-5.

Nice M.M. - Trans. Linn. Soc. N.Y., 1962, 8, p. 1-211.

Paganelli C.V. - Amer. Zool., 1980, 20, p. 329-338.

Piiper J., Tazawa H., Ar A., Rahn H.-Respir. Physiol.,1980,39, p.273-284.

Seymour R.S., Ackerman R.A. - Amer. Zool., 1980, 20, p. 437-447.

Seymour R.S., Rahn H. - In: Respiratory Function in Birds, Adult and Embryonic / Ed. by J.Piiper. Berlin, Heidelberg, New York: Springer-Verlag, 1978, p. 243-246.

Tazawa H. - Amer. Zool., 1980, 20, p. 395-404.

Visschedijk A.H.J. - Br. Poultry Sci., 1968, 9, p. 185-196.

Visschedijk A.H.J. - Amer. Zool., 1980, 20, p. 469-476.

Vleck C.M., Vleck D., Hoyt D.F. - Amer. Zool., 1980, 20, p. 405-416.

Walsberg G.E. - Amer. Zool., 1980, 20, p. 363-372.

PHYSIOLOGICAL CORRELATES OF SYNCHRONOUS HATCHING
IN RHEA EGGS (<u>RHEA AMERICANA</u>)

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INTRODUCTION

An individual bird does not lay more that one egg per day, therefore the
ages of eggs within a clutch usually vary. In spite of this, in many species
of precocial birds, all of the ages within a clutch hatch synchronously,
i.e., over a relatively short period of time. In most species of birds in
which hatching synchrony occurs, including quail, ducks, pheasants, and
grouse, incubation periods of individual eggs do not very by more than 1 or
2 days, normally less than 10% of the incubation period. Most of the synch-
rony in these clutches is due to parental delay in beginning incubation.
However, in a few species, incubation begins before the last egg is laid,
and synchrony is produced by social interaction between developing embryos.
One such species is the Common Rhea (<u>Rhea americana</u>).

The male Rhea (who does all of the incubating) begins incubation within
2-3 days after the beginning of egg-laying. Groups of 2-15 females continue
to deposit eggs in a male's nest for up to 12 days and then usually move on
to another male. As a result, incubation age of individual eggs in a clutch
may vary by 10 days, yet most of the 20-50 eggs in a clutch normally hatch
within a few hours of each other (Faust, 1960; Bruning, 1973a, 1974). The
incubation period, defined as the number of days an egg is maintained at a
high and constant temperature (35.5-37° C in the Rhea), varies from a mean
of 37 days to as little as 29 days and as much as 43 days (Faust, 1960;
Bruning, 1974). That is, embryonic development can be completed in as little
as 80% of the average incubation period or can be prolonged an extra 15%
beyond the normal hatching time. The magnitude of variability in incubation ·
period, on both relative and absolute scales, makes the Common Rhea an ideal
species for the study of the developmental consequences of synchronous
hatching.

ADAPTIVE VARIATION IN INCUBATION PERIOD

Synchronous hatching is advantageous in precocial species because it en-
ables the parent bird to make a rapid transition from behavior appropriate
for incubation to the very different behavior appropriate for the care of
mobile hatchlings. However, natural selection will favor embryos that
shorten (or perhaps  lengthen) their incubation period only when the bene-
fits of so doing outweigh the costs. It is likely that for each individual
there is some optimal incubation period, all other things being equal. By
leaving the egg too early the underdeveloped chick risks inadequate prepa-
ration for life as a hatchling, while delaying past the optimum time of
hatching places excessive demands on energy, water, and nutrient resources
within the egg that would otherwise be available for post-hatching growth
and activity. Of course, for individual eggs in a clutch, all other things

are not equal. Fitness of individuals will also depend on other members of the clutch and on interactions with the parent bird.

After their eggs begin to hatch, incubating male Rheas must choose between two mutually exclusive courses of action. They can continue incubating, in order to maximize the number of eggs that hatch, or they can lead the hatchlings away from the nest and ensure them early access to food under parental protection. The longer hatchlings remain at the nest, the more they deplete their energy and nutrient reserves, which can be replaced only by feeding. Natural selection should favor adults that leave the nest as soon as the probability of decreasing reproductive success due to loss of existing hatchlings exceeds the probability of increasing reproductive success by hatching more eggs. Male Rheas in the field behave in a way that is consistent with such an optimization process. Incubating males remain on the nest for only 24-36 hours after the first eggs hatch. They then lead the hatchlings away from the nest, and abandon any unhatched eggs (Bruning, 1974).

This adult behavior results in powerful selection for hatching synchrony within the clutch. Abandoned eggs cool and rarely hatch, and any that do hatch are subject to almost certain predation without the protection conferred by an accompanying adult (Bruning, 1974). Consequently, adaptations resulting in the capability to accelerate hatching to permit leaving the nest with the rest of the clutch and the adult will always be favored, as long as the developmental costs of accelerating hatching are less than lethal.

For the most advanced embryos, delaying hatching may be beneficial because it could permit conservation of energy and nutrient reserves. Chicks expend metabolic reserves at a rate more than twice that of full-term embryos still in the egg (Vleck, 1978) so it may be to an individual's advantage to delay hatching, rather than hatching long before the male leaves the nest. We have no data on Rheas, but Smit (1963) states that Ostrich hatchlings held longer than three days without food become weak.

SOCIAL ENVIRONMENT AND SYNCHRONIZING MECHANISMS

Hatching synchrony requires that embryos receive information about the developmental status of neighboring eggs and that rate of development vary with social environment of the embryo. Precisely how and when such changes in the developmental program occur are unknown although the information exchange between eggs is probably via auditory communication as has been demonstrated in several other species. There may be auditory input from the incubating adult as well (Hess, 1972). Nevertheless, because synchrony of hatching does occur under artificial incubation in Rheas (Faust, 1960; Bruning, 1974; Vleck et al., 1980), communication between eggs alone must be sufficient to produce alteration of the developmental program.

Most of the information on auditory communication between eggs and hatching synchrony comes from the work of Margaret Vince and her associates. All of the eggs within a clutch of Bobwhite Quail (Colinus virginianus) or Coturnix Quail (Coturnix coturnix japonica) normally hatch within a few hours. This synchrony is maintained even when some eggs in the clutch have been incubated for 24 hours more or less than the others (Vince, 1964a, b, 1968a). Hatching time can be accelerated, and total incubation period reduced, if

younger eggs are placed in contact with older ones (Vince, 1964a, b, 1973a; Vince, Chinn, 1971). It is also possible to retard hatching and increase incubation period by surrounding older quail eggs with younger ones (Vince, 1968a; Vince, Cheng, 1970; Freeman, Vince, 1974), but in general it is easier to accelerate hatching than to retard it. Ducks, geese, and chickens do not synchronize hatching as precisely as quail, but the spread of hatching times is less in eggs incubated together than in eggs incubated in isolation (B'jarvall, 1967; McCoshen, Thompson, 1968a) and hatching can be accelerated by external acoustic stimulation in these species also (Vince, 1973a; Vince et al., 1970).

Embryos of quail, chickens, and ducks produce sounds within the egg surprisingly early in incubation, and several of these sounds are known to influence hatching times of adjacent eggs (Orcutt, 1974). The first sounds produced are low-frequency, low-intensity sounds produced by the irregular movements of the developing embryos (Vince, Salter, 1967). Vince (1973b) played tape recordings of such low-frequency sounds to isolated Bobwhite eggs and demonstrated delayed hatching and prolonged incubation. Near the end of incubation, pulmonary respiration begins, producing low frequency pulses at a regular rate. Artificial sounds with the same pulse rate delay hatching in Bobwhite, but do not affect Coturnix (Vince, 1968b, 1973b). Sometime after pulmonary respiration begins, embryos of all species studied so far begin to produce intermittant high-amplitude clicking sounds (Driver, 1965; Vince, 1966a; McCoshen, Thompson, 1968b). These clicks are also produced by pulmonary respiration, but differ in both frequency and amplitude from the pulmonary sounds mentioned above. Loud artificial clicks over a wide range of pulse rates accelerate hatching in quail and chickens (Vince, 1966b, 1968b; Vince et al., 1970, 1971; Woolf et al., 1976), and the respiratory clicks presumably function in the same way. After initiation of pulmonary respiration, embryos begin to vocalize (Collias, 1952; Gottlieb, Vandenbergh, 1968; Hess, 1972; Beaver, 1978) but as yet there is no quantitative evidence that vocalizations are important in hatching synchrony.

It is likely that acoustic stimuli similar to those described in other precocial birds are responsible for hatching synchrony and consequent variation in incubation period in Rheas. Bruning (1973a, b; 1974) found that Common Rhea incubation could be shortened to as little as 29 days if young eggs were placed with older eggs for the two weeks before hatching. Rhea embryos produce audible clicks several days before hatching (Vleck, unpubl. observation) and begin to vocalize after penetration of the air cell (Bruning, 1974). Beaver (1978) described a "contact-whistle" vocalization in Rhea hatchlings and stated the same sound is produced by embryos in the air cell before hatching.

Social contact between embryos is apparently very important in stimulating hatching in Rheas. Hatchability of eggs incubated in isolation is very low (Vleck, unpubl. observation). Bruning (1974) reported that only 25% of isolated eggs hatched whereas 85% of eggs incubated in groups hatched. Isolated eggs that did hatch did so only after 41 days of incubation, rather than the 36-37 days typical of eggs incubated in groups.

In Rheas, hatching synchrony is produced by variations in incubation period between eggs within a clutch. Consequently, the developmental program must vary between individuals. In order to study embryonic development, ideally one should investigate the physiological and anatomical progress of the embryo directly. However, because we had access to a limited number of Rhea eggs, a direct study of embryo growth was not feasible. Instead, we measured rate of oxygen consumption using techniques described in D.Vleck et al. (1980) as an index of embryo growth and development. Such measurement of metabolic rate is a noninvasive technique with which growth and development can be monitored continuously throughout ontogeny in a single egg.

Energy expenditure (metabolism) in a developing embryo is devoted primarily to two processes: biosynthesis of new tissue, or growth, and maintenance of existing tissue. The metabolic rate of a growing embryo is the sum of the energy costs of growth, which increase with absolute growth rate; and the energy costs of maintenance, which increase with embryo mass. We previously described the relationship between metabolic rate, absolute growth rate, and embryo mass in a number of bird species and showed that ontogeny of metabolism varies with growth pattern in avian eggs (C.Vleck et al., 1980). In altricial species both metabolic rate and growth rates of embryos increase continuously and at an accelerating rate throughout incubation. In precocial species embroys initially grow at a increasing rate, but reach hatchling mass as early as 80% of the way through incubation and growth rate then declines. Metabolic rates of embryos of precocial species increase rapidly until about 80% through incubation and then increase slowly, remain constant, or even decline as the metabolic expenditure devoted to growth declines.

In the Common Rhea, rate of oxygen consumption increases exponentially through the first 25 days of incubation, with little variability between eggs of the same age. Metabolic rate reaches a maximum after about 29 days of incubation, then usually declines to about 70% of the maximum value and remains low until just before hatching (Figure 1). Metabolic rate increases when the embryo penetrates the air cell and increases again after pipping.

The ontogeny of metabolism in Rhea embryos is consistent with the following growth pattern (Figure 2). Growth rate increases continuously, perhaps exponentially, over the first 70% of incubation. Growth rate and therefore metabolic expenditure for growth then decline rapidly, resulting in the decline in total metabolic rate. We suggest that tissue growth of the Rhea embryo is nearly complete at the time of the peak in metabolic rate, and that the remainder of incubation is used for metabolically inexpensive processes like maturation of neural and sensory functions. One Rhea embryo that died after 31 days of incubation appeared fully developed and was the same size as hatchlings. In Emus (Dromaius novae-hollandiae) and Ostriches (Struthio camelus) that have similar ontogenies of metabolism to that of the Rhea (Hoyt et al., 1978; D.Vleck et al., 1980) embryos that died about 80% of the way through incubation (at the tims we suggest growth is complete) also appeared fully developsd sxternally and had yolk-free body masses equal to those of successful hatchlings (Vleck, 1978).
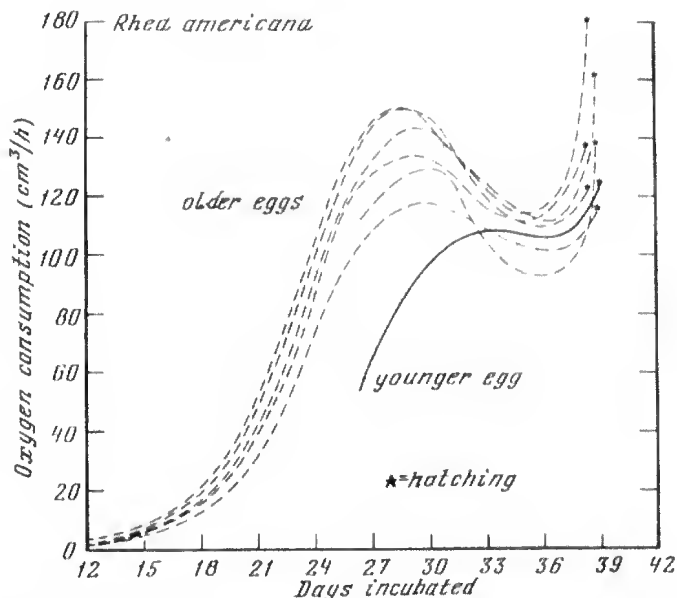
F i g. 1. Rates of oxygen consumption during development of seven Common
Rhea eggs incubated together. Six eggs were the same age (dashed lines)
and one egg was four days younger (solid line). Time of hatching is in-
dicated by a star (Redrawn from D.Vleck et al., 1980)

The period after completion of tissue growth, between the peak in metabo-
lic rate and hatching, appears to be the period that can be shortened or
lengthened to permit hatching synchrony in Rheas. This suggestion is sup-
ported by two observations. First, the shortest reported incubation period
for Common Rhea eggs is 29 days (Bruning, 1974), coinciding with the peak of
metabolism, that time at which we suggest growth is nearly complete. Second,
the pattern of metabolism of eggs that are stimulated to hatch early does not
differ from the "normal" pattern described above until near the time of the
peak in metabolic rate.

We accelerated hatching in some Rhea eggs by placing young eggs in an in-
cubator in contact with a group of four to six older eggs. When one Rhea egg
was placed with six other eggs that were four days older, the younger egg had
a peak metabolic rate about four days later than the older eggs, but its me-
tabolic rate did not then decline significantly (Figure 1). The rate of oxygen
consumption in this egg increased at the same time that the older eggs showed
the typical pre-pipping increases in metabolism, although it did not pip un-
til 24 hours later. Five of the other six eggs hatched essentially synchro-
nously during a 9.4 hr interval, and the sixth egg hatched the following day.
Ontogeny of metabolism of the accelerated egg paralleled that of the older
eggs until the time of peak metabolism. It hatched 6 days post-peak while
the six older eggs hatched 10 days post-peak. We suggest that the absence of
a decline in metabolic rate in the younger egg resulted from a relatively
higher growth rate during the last few days of incubation, just as one would
expect in an embryo trying to "catch up" with its nestmates.
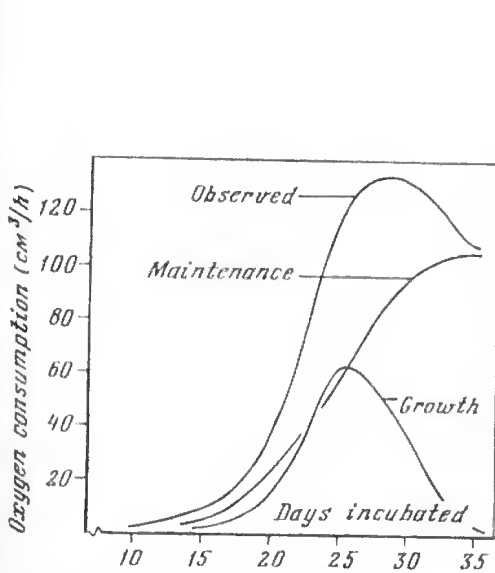
F i g. 2. Observed rate of oxygen consumption during development of Common Rhea embryos and probable allocation of metabolic expenditure to growth and maintenance metabolism. Growth and maintenance curves are drawn so that their sum equals the observed metabolic rate. We assumed that energy used for maintenance is proportional to embryo mass, which is near its maximum after about 29 days of incubation. Tissue growth rate and costs of growth decline after this time
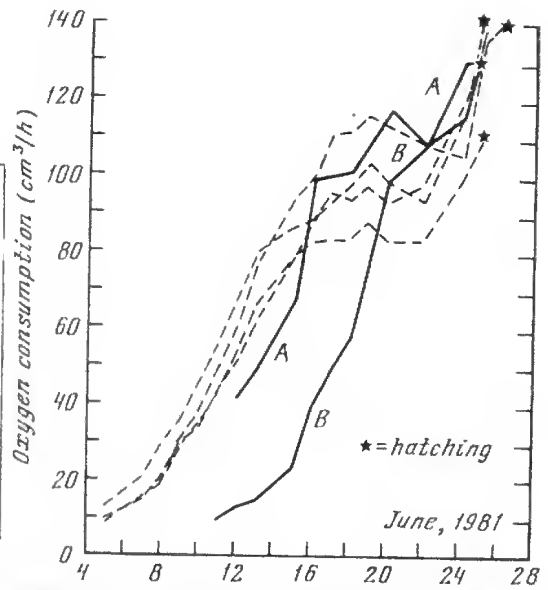
F i g. 3. Rate of oxygen consumption as a function of calander date for six Common Rhea embryos incubated together. Four eggs were the same age (dashed lines) and two eggs (labeled A and B, solid lines) were younger. Stars indicate time of hatching

In another experiment four Rhea eggs of the same age were incubated with two younger eggs of unknown age. When metabolic rate of each egg is plotted as a function of calendar date (Figure 3) it is clear that during the early part of incubation the two younger eggs (A and B) had lower metabolic rates than the older eggs measured on the same day, presumably because the younger embryos were smaller. Three of the older eggs hatched within four hours of each other on June 25 and younger egg A hatched during this time as well. The next day the remaining older egg hatched and the embryo in egg B was dead. When we opened egg B, the embryo appeared fully developed and had completely withdrawn the yolk sac into the abdominal cavity. This embryo had probably attempted to begin the hatching process the previous day as indicated by a large increase in its metabolic rate on  June 25 (Figure 3).

We can estimate the actual number of days that Rhea eggs have been incubated from the metabolic measurement made in the first two-thirds of incubation. This is because within a species there is little variability in metabolic rates of eggs of the same incubation age during early development, when embryo sizes and growth rates are independent of egg size. By super-
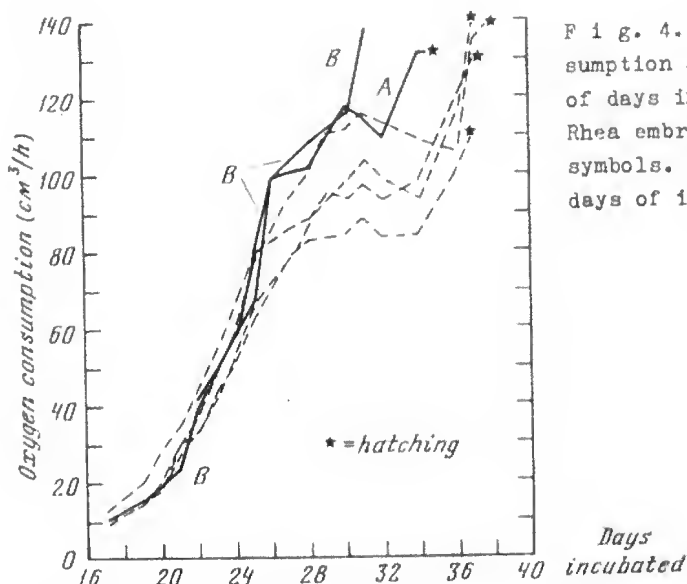
F i g. 4. Rate of oxygen consumption as a function of number of days incubated for six Common Rhea embryos. See Figure 3 for symbols. Egg B died after 31 days of incubation

imposing the early data from eggs A and B over that of the eggs of known age (Figure 4) we can estimate that egg A was two days younger in incubation age than the others and egg B was seven days younger. Yet they hatched or attempted to hatch synchronously with the older eggs. That is, whereas the four older eggs hatched after 37 days of incubation, egg A hatched after 35 days, and egg B attempted to hatch after 31 days of incubation. After day 26 of incubation, the accelerated eggs hat higher rates of oxygen consumption, and therefore presumably higher growth rates, than most unaccelerated eggs incubated for the same amount of time (Figure 4). Presence of older eggs apparently stimulates growth of younger embryos, making early hatching possible.

## CONSEQUENCES OF VARIATION IN INCUBATION PERIOD

To hatch successfully, avian embryos must attain a minimum level of physiological, morphological, and behavioral competence. When incubation period varies within a species, some embryos have less time to develop this minimum competence than others. The adaptive benefits of synchronous hatching are clear but the nature of any costs that are consequent to attaining hatching synchrony by altering the time spent in embryonic development remains an open question.

Quail embryos whose hatching time is advanced by acoustic stimulation are not smaller than those with normal incubation periods (Vince, 1969; Grieve et al., 1973). This is not surprising because tissue growth rate of a precocial embryo is low during the last few days of incubation (Romanoff, 1967; Vleck et al., 1980) and because any nutrients not converted to embryonic tissue are retained by the hatchling as yolk. There are some suggestions, but almost no quantitative evidence, that early or late hatching chicks are less fit than chicks that hatch at the 'optimal' time. One of our Rhea embryos that apparently attempted to hatch after only 31 days of incubation subsequently died in the shell. In quail, eggs whose hatching time is accelerated or retarded produce weaker chicks with lower viability than eggs

870

that hatch after the normal incubation time (Vince, 1969; Vince, Chinn,1971; Grieve et al., 1973). Late Rhea hatchlings often have developmental abnormalities (Bruning, 1973b). A curled toe syndrome in late hatching quail may result from prolonged containment within the shell after growth is complete (Vince, 1969). Coturnix that hatch early are often weaker, begin to stand later after hatching, and have slightly higher incidence of abnormal posture than those hatching after the normal incubation period (Vince, Chinn, 1971). Vince (1973c) proposed that the clicking sound associated with pulmonary ventilation may act like a cough and function in clearing fluid from respiratory passages. Chicks that hatch early, after 'clicking' for relatively short periods, may be less efficient in ventilation and therefore weaker.

Because the absolute amount of time by which the incubation period in the Rhea can be altered is so large, further study of this species will provide an opportunity to examine the ecological consequences of synchronous hatching. Is there an optimum incubation period and do embryos that hatch sooner or later than this optimum pay a price for synchronizing hatching? We need to know more about the morphological, physiological, and behavioral consequences to the hatchling of variation in incubation period. This will provide insight into the adaptive trade-offs involved in the evolution of synchronous hatching.

## SUMMARY

The male Common Rhea begins incubation of eggs before the clutch is complete, yet all the eggs normally hatch within a few hours of each other. Synchronous hatching is advantageous because it allows the male to switch immediately from incubation of eggs to care of mobile hatchlings. However, synchronous hatching requires that the last-laid eggs must accelerate development and hatching to permit leaving the nest with the rest of the clutch. Incubation periods of individual eggs can vary from the mean of 37 days to as little as 29 days or as many as 42 days. The mechanism allowing synchronization of hatching is probably auditory communication between embryos during the last part of incubation. We studied the process by which embryos synchronize hatching by monitoring metabolic rate of eggs through development. In eggs with an incubation period of 37-39 days, metabolic rate, as measured by oxygen consumption, increases exponentially during the first 70% of incubation, reaches a maximum on day 29, then declines until shortly before hatching. Embryonic tissue growth is essentially complete on day 29, and the decline in metabolic rate appears to be due to a decline in growth rate. However, this period of decline can be shortened or eliminated to allow synchrony of hatching. The pre-hatching decline in metabolic rate is absent in eggs that are incubated with older eggs and consequently hatch after a shorter incubation period. The relatively high metabolic rate in these eggs at this time is presumably due to the cost of accelerated development. The morphological, physiological, and behavioral consequences to the hatchings of variation in incubation period requires further investigation.

## ACKNOWLEDGMENTS

References

Beaver P.W. - Auk, 1978, 95, p. 382-388.
B'Jarvall A. - Behav., 1967, 28, p. 141-148.
Bruning D.F. - Nat. Hist., 1973a, 82, p. 68-75.
Bruning D.F. - Intern. Zoo. Yearbook, 1973b, 13, p. 163-171.
Bruning D.F. - Living Bird, 1974, 13, p. 251-294.
Collias N.E. - Auk, 1952, 69, p. 127-159.
Driver P.M. - Nature, 1965, 206, p. 315.
Faust R.  Verhandl. Deutsch. Zool. Gesellsch., 1960, 42, p. 398-401.
Freeman B.M., Vince M.A. - Development of the Avian Embryo. New York: Wiley,
    1974.
Gottlieb G., Vandenbergh J.G. - J. Exp. Zool., 1968, 168, p. 307-326.
Grieve B.J., Wachob R., Peltz A., VanTienhoven A. - Poult. Sci., 1973, 52,
    p. 1445-1450.
Hess E.H. - Sci. Am., 1972, 227, p. 24-31.
Hoyt D.F., Vleck D., Vleck C.M. - Condor, 1978, 80, p. 265-271.
McCoshen J.A., Thompson R.P. - Can. J. Zool., 1968a, 46, p. 243-248.
McCoshen J.A., Thompson R.P. - Can. J. Zool., 1968b, 46, p. 169-172.
Orcutt A.B. - Behav., 1974, 50, p. 173-184.
Romanoff A.L. Biochemistry of the Avian Embryo. N.Y.: Wiley, 1967.
Smit D.J.v.Z. Ostrich farming in the little Karoo. - In: Bull. N 358
    Department of Agricultural Technical Services. Pretoria, 1963.
Vince M.A. - Anim. Behav., 1964a, 12, p. 531-534.
Vince M.A. - Nature, 1964b, 203, p. 1192-1193.
Vince M.A. - Anim. Behav., 1966a, 14, p. 34-40.
Vince M.A. - Anim. Behav., 1966b, 14, p. 389-394.
Vince M.A. - Anim. Behav., 1968a, 16, p. 332-335.
Vince M.A. - Brit. Poult. Sci., 1968b, 9, p. 87-91.
Vince M.A. - In: Bird Vocalization / Ed. by R.A.Hinde. Cambridge: Cambridge
    Univ. Press, 1969, p. 233-260.
Vince M.A. - Brit. Poult. Sci., 1973a, 14, p. 389-401.
Vince M.A. - In: Behavioral Enbryology / Ed. by G.Gottlieb. N.Y.: Acad.
    Press, 1973b, p. 285-323.
Vince M.A. - Comp. Biochem. Physiol., 1973c, 44A, p. 341-354.
Vince M.A., Cheng R.C.H. - Anim. Behav., 1970, 18, p. 210-214.
Vince M.A., Chinn S. - Anim. Behav., 1971, 19, p. 62-66.
Vince M.A., Green J., Chinn S. - Brit. Poult. Sci., 1970, 11, p. 483-488.
Vince M.A., Green J., Chinn S. - Comp. Biochem. Physiol., 1971, 39A,
    p. 769-783.
Vince M.A., Salter S.H.A. - Nature, 1967, 216, p. 582-583.
Vleck C.M., Vleck D., Hoyt D.F. - Am. Zool., 1980, 20, p. 405-416.
Vleck D. The energetics of activity and growth. Ph.D. Thesis, Univ. of
    California, Los Angeles, 1978.
Vleck D., Vleck C.M., Hoyt D.F. - Physiol. Zool., 1980, 53, p. 125-135.
Woolf N.K., Bixby J.L., Capranica R.R. - Sci., 1976, 194, p. 959-960.

# HETEROGENEITY OF EGGS AND HETEROCHRONY OF AVIAN EMBRYOS DEVELOPMENT UNDER INCUBATION IN NATURE

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## EGG HETEROGENEITY IN A SINGLE CLUTCH

An ever increasing attention is being paid in poultry raising to the biological properties of the eggs of domestic birds. Eggs selected for incubation are estimated by their mass, form, vitamin content of and other indices. The survival of embryos and nestlings of domestic birds was shown to depend on the incubation (biological) properties of eggs.

Thus, in a few ornithological studies the attention was drawn to the relationship of some egg parameters, mainly egg mass in the clutch, with the hatchability of nestlings (Parsons, 1970, 1971; Syroechkovsky., 1975, etc.). Studies of morphological, biochemical, biophysical parameters of egg clutches in avian species from different orders (Bolotnikov et al.,1977, 1978, 1980) fill in, to a considerable extent, the gap in this problem.

Egg morphology. Among of morphological parameters, the volume and mass of the egg and its contains were under study. It was established that the mean values of these indices show a tendency to decrease from the first egg in the

T a b l e 1. Morphological Characteristics of Eggs with Reference to the Sequence of Their Laying

| Feature | | n | Sequence of Egg Laying | | | |
| --- | --- | --- | --- | --- | --- | --- |
| | | | First | | Last | |
| | | | $\bar{x}{\pm}m$ | C% | $\bar{x}{\pm}m$ | C% |
| | | | *Larus* canus | | | |
| Volume $10^{-6}$ | $m^3$ | 76 | 54.80±0.50 | 8.1 | 53.33±0.67 | 8.8 |
| Mass $10^{-3}$ | kg | 13 | | | | |
| | egg | | 58.02±0.92 | 5.8 | 56.64±1.28 | 8.2 |
| | yolk | | 13.42±0.36 | 9.6 | 12.78±0.33 | 9.2 |
| | albumen | | 40.98±0.67 | 5.9 | 40.35±1.08 | 9.8 |
| | shell | | 3.60±0.08 | 7.8 | 3.48±0.07 | 6.8 |
| | | | *Corvus* frugilegus | | | |
| Volume $10^{-6}$ | $m^3$ | 40 | 15.66±0.27 | 10.6 | 14.23±0.26 | 11.5 |
| Mass $10^{-3}$ | kg | 10 | | | | |
| | egg | | 16.41±0.56 | 11.0 | 14.85±0.72 | 15.0 |
| | yolk | | 1.93±0.078 | 13.0 | 1.89±0.07 | 12.0 |
| | albumen | | 13.53±0.55 | 13.0 | 12.08±0.067 | 18.0 |
| | shell | | 0.98±0.03 | 10.0 | 0.89±0.029 | 10.0 |
| | | | *Columba* livia | | | |
| Volume $10^{-6}$ | $m^3$ | 36 | 16.42±0.22 | 8.0 | 16.24±0.23 | 8.3 |
| Mass $10^{-3}$ | kg | 9 | | | | |
| | egg | | 17.03±0.49 | 9.0 | 16.40±0.49 | 9.0 |
| | yolk | | 2.72±0.099 | 11.0 | 2.54±0.096 | 11.0 |
| | albumen | | 13.14±0.413 | 9.0 | 12.78±0.406 | 10.0 |
| | shell | | 1.16±0.04 | 11.0 | 1.07±0.03 | 9.0 |

clutch to the last one (Table 1). But this pattern is not absolute. E.g , a decrease in the egg volume, mass and components from the first eggs to the last ones was observed in Larus canus in 68%, in Columba livia in 70% and in Corvus frugilegus in 85%. The mass of yolk in the first eggs was greater than in the last ones in 60% of nests in the common gull, 88% in the rock dove and 70% in the rook.

The quantitative estimate of calcium carbonate content in the egg shell was carried out with consideration to the place of egg in the egg laying cycle. The variations of these values (Table 2) do not allow us to draw de-

T a b l e  2. Calcium Carbonate Content in the Egg Shell, %

| Species | n | Sequence of Egg Laying | |
|---|---|---|---|
| | | First $\bar{x}\pm m$ | Last $\bar{x}\pm m$ |
| Larus canus | 15 | 82.3±1.1 | 82.0±1.0 |
| Columba livia | 31 | 86.2±0.4 | 87.7±0.4 |
| Corvus frugilegus | 25 | 76.3±1.8 | 85.4±2.1 |
| Passer montanus | 10 | 68.7±1.9 | 69.8±3.5 |
| Turdus pilaris | 15 | 78.1±1.4 | 75.1±2.2 |

finite conclusions, except for the rook, on egg heterogeneity within the clutch by this parameter. Interspecific differences were also hardly expressed at all. One can only suggest that in birds with a relatively short period of embryogenesis the degree of shell mineralization is lowered and rarely exceeds 80%.

Concentration of hydrogenic ions (pH). In the eggs of avian species pH is interest both for their characteristic and possible estimation of their heterogeneity. Eggs of the common gull and of the rock dove were studied in this respect. In the former, the eggs of three groups of clutches were studied in which the first eggs appeared, respectively, on May 8, 11 and 16. A tendency was found to changes in pH of yolk and albumen in the eggs of the same clutch (Table 3). In most of the clutches, pH in the first eggs was somewhat lower

T a b l e  3. The Dependence of pH of Egg Components in Larus canus on the Time of Clutch Formation (n = 12 for every day)

| Time of Appearance of Clutches | Egg Component | First Eggs $\bar{x}\pm m$ | Third Eggs $\bar{x}\pm m$ | t-criteria |
|---|---|---|---|---|
| May 8 | Yolk | 6.18±0.09 | 6.47±0.09 | 2.4 |
| May 11 | | 6.30±0.04 | 6.49±0.06 | 2.7 |
| May 16 | | 6.03±0.14 | 6.27±0.12 | 1.3 |
| May 8 | Liquid Albumen | 8.37±0.04 | 9.76±0.06 | 6.0 |
| May 11 | | 8.47±0.06 | 8.78±0.10 | 2.5 |
| May 16 | | 8.66±0.04 | 8.70±0.10 | 0.4 |
| May 8 | Dense Albumen | 8.55±0.07 | 8.71±0.08 | 1.5 |
| May 11 | | 8.45±0.06 | 8.84±0.08 | 3.9 |
| May 16 | | 8.47±0.04 | 8.72±0.09 | 2.6 |

than in the third (at  t = 2). No distinct differences were found with res-
pect to the time of laying and sequence of eggs.

In the rock dove the reproductive period lasts from February till Septem-
ber and can involve, in town, five cycles of breeding. pH differed in the
eggs of different cycles (Table 4).

Indices of **yolk** and  **albumen**. The index of albumen is, to a certain ex-
tent, a criterion of hatchability of nestlings. As noted by B.A.**Sergeyev** and

T a b l e   4. pH of Yolk and Albumen in the Eggs of <u>Columba livia</u> During
Different Cycles of the Reproductive Period (n = 15 for every month)

| Time of Formation | Egg Component | First Eggs $\bar{x}+m$ | Second Eggs $\bar{x}+m$ | t-criterion |
|---|---|---|---|---|
| February | Yolk | 5.93+0.05 | 5.89+0.05 | 0.6 |
| | Albumen liquid | 9.00+0.02 | 8.30+0.04 | 15.5 |
| | Dense | 8.72+0.07 | 8.41+0.12 | 2.2 |
| April | Yolk | 5.50+0.02 | 5.80+0.14 | 2.1 |
| | Albumen liquid | 8.42+0.02 | 8.52+0.03 | 2.5 |
| | Dense | 8.60+0.05 | 8.50+0.07 | 1.1 |
| June | Yolk | 5.50+0.02 | 5.80+0.14 | 2.1 |
| | Albumen liquid | 8.42+0.02 | 8.52+0.03 | 2.5 |
| | Dense | 8.39+0.05 | 8.42+0.05 | 1.4 |

V.D.Sergeyeva (1964), the increased amount of albumen is correlated with a mar-
ked increase of its index and, as a rule, eggs with a higher albumen index have
also a higher yolk index. The decrease of albumen index indicates the in-
crease of water content in the egg albumen. These indices were determined
in three unrelated avian species (Table 5).

Water content in the albumen in the common gull is 4 times that in the
yolk judging by the ratio of indices but the heterogeneity of eggs according
to these indices was not found. In the rock dove the heterogeneity of eggs
is distinctly expressed in the lower values of yolk and albumen indices of
the last eggs as compared with the first ones. A comparison of yolk indices
in the rook eggs has shown different (by sequence) eggs. Relatively high
yolk indices, as compared with two former species, appear to be due to a
stronger yolk membrane.

Carotinoid and vitamin A content. The biological value of eggs directly
depends on the vitamin A and carotinoid content in the yolk (Eremeyev, 1957,
etc.). Vitamin A has a wide range of action. Carotinoids provide for the

T a b l e   5. The Values of Yolk and Albumen Indices with Respect to the
Sequence of Eggs in the Clutch

| Species | n | First Eggs | | Last Eggs | |
|---|---|---|---|---|---|
| | | Yolk | Albumen | Yolk | Albumen |
| Larus canus | 37 | 0.383+0.003 | 0.090+0.001 | 0.385+0.005 | 0.090+0.002 |
| Columba livia | 31 | 0.379+0.002 | 0.054+0.002 | 0.368+0.004 | 0.048+0.001 |
| Corvus frugilegus | 20 | 0.457+0.008 | - | 0.427+0.008 | - |

Table 6. Carotinoids and Vitamin A Content in the Egg Yolk in _Corvus frugilegus_ (ug/g)

| Index | Sequence of the Egg | $\bar{x}\pm m$ | Lim |
|---|---|---|---|
| Total Carotinoids | 1 | 11.24±0.62 | 7.97±14.97 |
| | 4 | 6.25±0.53 | ·3.51±9.99 |
| Vitamin A | 1 | 10.80±0.29 | 9.73±12.28 |
| | 4 | 4.26±0.32 | 3.00±5.83 |

adaptive character of responses of the organism to life conditions and increase the general level of its viability. Eggs of the same clutch were shown to be heterogenous by these parameters as well (Table 6).

The differences in vitamin A and carotinoid content between the first and fourth eggs in the clutch are statistically reliable (p = 0.0001). These indices proved to be the most variable in the last eggs as compared with the first ones. Low carotinoid and vitamin A content in the last eggs of the clutch appears to be one of the causes of increased embryonic mortality in the rook.

Egg strength. The strength of eggs equals, according to approximated data, 1063 km/m$^3$ in the common gull, 1055 km/m$^3$ in the rook, and 1040 km/m$^3$ in the sand martin. The strength of eggs in the same clutch varied and, hence, this index can be used to characterize the heterogeneity of eggs (Table 7).

Heterogeneity of eggs and survival of birds. A high degree of mortality of the embryos and nestlings is observed in birds, ca. 40% (Malchevsky, 1959). The rook is also characterized by a high mortality rate during the nest period: 15-20% in embryos and 30-35% in nestlings (Bolotnikov et al., 1973). In this species mortality rate early ontogenesis is related to egg heterogeneity in the clutch. Such a dependence is also found in the common gull and sand martin. E.g., the clutches in the centre of the common gull colony are characterized by a greater egg volume as compared with its periphery (57.0 x 10$^{-6}$ m$^3$ vs. 54.7 x 10$^{-6}$ m$^3$). The survival of nestlings varied as well. In the colony centres 97% of nestlings survived till the moment of flight from the first eggs, 88% from the second eggs and 68% from the third eggs. And the level of mortality was distinctly higher in the colony periphery where the survival rate equalled 78 % for the first and second eggs and only 50% for the third ones.

In the sand martin nestlings the mortality from the small eggs exceeded the large ones by 3.5 times (Bolotnikov, Marks, 1980).

Table 7. The Strength of the Eggs from the Main and Resumed Clutches in _Corvus frugilegus_

| Sequence of Egg Laying | n | Main Clutches $\bar{x}\pm m$ | C% | Egg Strength kg/m$^3$ | $\bar{x}\pm m$ | Resumed Clutches C% |
|---|---|---|---|---|---|---|
| 1 | 23 | 1053 | 0.6 | 24 | 1057 | 1.8 |
| 2 | 21 | 1051 | 0.7 | 13 | 1057 | 1.1 |
| 3 | 18 | 1047 | 0.08 | 10 | 1056 | 1.3 |
| 4 | 16 | 1047 | 0.04 | 7 | 1062 | 1.1 |
| 5 | 6 | 1047 | 0.3 | 4 | 1065 | 0.5 |

Eggs of the same clutch are thus heterogenous due to a complex of morpho-
logical, biochemical and biophysical parameters. One can suggest that the
heterogeneity eggs provides for phenotypical heterogeneity of embryos and
nestlings and is, probably, involved in the regulation of the population
density.

HETEROCHRONIES OF EMBRYONIC DEVELOPMENT
IN EGGS OF THE SAME CLUTCH

Birds are usually divided into three groups by the initial phase of in-
cubation: 1) incubating after egg laying completion (Anseriformes, Galli-
formes); 2) incubating beginning with the first egg (Strigiformes, Falconi-
formes), and 3) incubating from the middle of egg laying (Piciformes, some
Passeriformes). It was believed that eggs for which the onset of incubation
coincided with the completion of egg laying could be in the state of diapause
20 to 30 days.

A study of incubation and embryogenesis undertaken in our laboratory al-
lowed us to propose another explanation for the initial stage of incubation
and made us doubt the presence in the eggs (more precisely, in the embryos)
of a long-term diapause (Bolotnikov et al., 1968, 1969, 1970, etc.). On
clutches of several dozens of birds (Anseriformes, Passeriformes, etc.) it
was convincingly proved that incubation proceeded from the first laid egg.
In some birds this process proceeds continuously, e.g. in Strigiformes, Fal-
coniformes, in others it is interrupted (Galliformes, Anseriformes), and, fi-
nally, in the third group the interrupted incubation at the beginning of egg
laying is combined with a relatively incubation towards its completion.

Analysis of total preparations of the early avian embryos revealed a com-
mon pattern: in the same clutch they were at different stages of growth and
development. It may be illustrated by characteristics of total preparations
of eight Anas crecca embryos (Table 8). It follows from Table 8 that there

Table 8. Morphological Characteristics of Embryos in Anas crecca

| Age | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| a) from the moment of egg laying, days | 8 | 7 | 6 | 5 | 4 | 3 | 2 | 1 |
| b) by the degree of development, hours | 64-68 | 58-62 | 57-60 | 55-58 | 54-57 | 50-54 | 36-40 | 20-30 |
| Stage of Development | 18⁻ | 17 | 17⁻ | 16+ | 16+ | 15+ | 12 | 10+ |
| Segmentation of Mesoderm (pairs of somites) | 32 | 29 | 28 | 27 | 27 | 25 | 16 | 11 |
| a) covered by amnion | 28 | 23 | 21 | 18 | 17 | 15 | 4 | 0 |
| b) not covered by amnion | 4 | 6 | 7 | 9 | 10 | 10 | 12 | 11 |
| Angle Between Fore- and Hind Brain | 45° | 45° | 45° | 52° | 54° | 90° | 120° | - |
| Length of embryo | 9.0 | 8.3 | 7.5 | 7.2 | 7.7 | 6.7 | 6.3 | 5.8 |
| Size of Yolk Sac Vascular Yield, mm | | | | | | | | |
| a) Length | 21.0 | 17.5 | 17.0 | 17.4 | 15.7 | 12.6 | 10.2 | 8.5 |
| b) width | 22.1 | 18.5 | 21.0 | 16.0 | 16.3 | 13.2 | 10.2 | 5.0 |

T a b l e  9. The Development of Embryos in the Same Clutch at the Beginning of Incubation

| Species | Nos. of Embryos Stage of Development | | | | | Difference in Stages Between the Extreme Variants | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | |
| Anas platyrhynchos | 18 | 17+ | 17 | 16+ | 16 | 14 | 10 | | | | 8 |
| A.strepera | 21 | 21- | 20 | 19+ | 19 | 18+ | 18+ | 17 | 16 | 14- | 7 |
| A.strepera | 19 | 18 | 18 | 18- | 17 | 17- | 17- | 16+ | 14 | 10 | 9 |
| A.querquedula | 24 | 24- | 23 | 23- | 22- | 22 | 22 | 21 | 10 | | 5 |
| A.querquedula | 21 | 20 | 19 | 18 | 17 | 16+ | 15 | 13+ | 10 | 6 | 15 |
| A.querquedula | 25 | 24+ | 24+ | 24 | 23 | 22 | 22- | 17 | | | 8 |
| Aythya ferina | 13 | 12 | 11+ | 10- | 10- | 9+ | 9- | 8- | | | 5 |
| A.ferina | 25 | 25 | 24 | 23 | 20 | 19 | 16+ | 16 | 13 | | |
| A.fuligula | 17 | 17 | 16 | 15 | 12 | 8- | 6 | | | | 11 |

T a b l e  10. The Age of Embryos and Degree of their Increase

| | Egg Laying | Embryo | from the moment of laying | by the degree of development |
|---|---|---|---|---|
| Riparia riparia | June 20 | 1 | 82 | 36-40 |
| | June 21 | 2 | 58 | 26-28 |
| | June 22 | 3 | 34 | 26-27 |
| | June 23 | 4 | 10 | 10 |
| Fringilla coelebs | June 13 | 1 | 110 | 48-50 |
| | June 14 | 2 | 86 | 43-45 |
| | June 15 | 3 | 60 | 42-44 |
| | June 16 | 4 | 38 | 26-28 |
| | June 17 | 5 | 14 | 14 |
| Phoenicurus phoenicurus | June 2 | 1 | 114 | 72-76 |
| | June 3 | 2 | 90 | 64-68 |
| | June 4 | 3 | 66 | 54-52 |
| | June 5 | 4 | 40-42 | 40-42 |
| Turdus iliacus | May 9 | 1 | 126 | 72-84 |
| | May 10 | 2 | 102 | 72 |
| | May 11 | 3 | 78 | 51-56 |
| | May 12 | 4 | 54 | 50-53 |
| | May 13 | 5 | 30 | 23-26 |
| | May 14 | 6 | 6-8 | 6-8 |

are differences between the embryos due to a complex of morphological features, for example, the embryo from the first egg was at stage 18 (according to Hamburger and Hamilton, 1951), while that from the last 8th egg - at stage 10.

Heterochronies were established in embryonic development of other Anas species (Table 9) and Passeriforms too. The total preparations of the latter were made during the first day after the completion of laying a four-egg clutch. The embryo from the first egg was at stage 11, while that

878

from the last egg-at stage 2 (primitive streak).

One more aspect **of the** phenomena taking place during incubation deserves consideration (Table 10). It follows from Table 10 that the embryos from the last eggs, in spite of their delay in development, were characterized by a higher rate of development. This effect was observed during the whole period of incubation from the moment of egg laying till the hatching of nestlings.

The incubation of eggs during the period of egg laying is of adaptive importance since it prevents mortality due to the effect of a long-term diapause (Bolotnikov et al., 1973; Shurakov, 1977).

These materials allow us to draw some general conclusions:

1. The results of studying morphological, biochemical and biophysical features and properties of eggs in birds of different taxa suggest their heterogeneity within the same clutch.

2. Egg heterogeneity provides for their biological (incubation) properties and determines, to a great extent, the level of hatchability.

3. In all avian species incubation is realized from the moment of the first egg laying, ensuring thus complete realization of the clutch.

4. Egg heterogeneity and heterochronies of embryogenesis provide for phenotypical heterogeneity of nestlings.

SUMMARY

The laying of eggs is characterised by heterogeneity according to morphological qualities of volume, mass, density, the content of carota and vitamin A, egg-white, yolk of egg and others. For instance, in a great number of cases the first egg of a laying Larus canus L. has mass (n=76; g) $58.02 \pm 0.92$ more than the third ($56.64 \pm 1.28$), yolk of egg $13.42 \pm 0.36$ and $12.78 \pm 0.33$, egg-white $40.98 \pm 1.08$, carota (n=12; mkg) $276.0 \pm 24.8$ and $174.0 \pm 28.9$, vitamin A $80.2 \pm 6.4$ and $48.1 \pm 6.9$ respectively. Heterogeneity of eggs has been shown in Columba livia Gmelin, Corvus frugilegus L. and other birds.

The process of natural incubation in many birds is started with the laying of the first egg continuously or interruptively, resulting in heterogeneity of the development of embryos. For instance, in Anas crecca L., the embryo of the 1st egg reached the 18th stage of development during the laying period, the 2nd and the 3rd - the 17th, the 6th - the 15th and the 8th - the 10th stage. The first embryo had 32 pairs of somites, the 8th - 11. They had other heterogeneous qualities.

Heterogeneity of the development of embryos of one clutch is better manifested when the birds have uninterrupted laying during the laying period. In this case the hatching takes place at different times. The incubation of eggs during the laying period has the adaptive meaning that is expressed in the preventing of elimination of embryos, uncapable of remaining in diapause.

Heterogeneity of eggs and heterochronia of the development of embryos call forth phenotypical variability of birds in early onthogenesis and has a selective meaning.

R e f e r e n c e s

Bolotnikov A.M., Shurakov A.I., Fedotova L.Ya. - Uch. Zap. Permskogo ped.
    in-ta, 1968, 58, p. 63-70.
Bolotnikov A.M., Shurakov A.I., Kamensky Yu.N., Korolev V.K. - In: Sb.statei
    po ptitsevodstvu i ornitologii. Perm, 1969, p. 50-66.
Bolotnikov A.M., Shurakov A.I., Kamensky Yu.N., Korolev V.K. - Ekologiya,
    1970, N 4,p. 40-46.
Bolotnikov A.M., Sokolova T.I., Chashchin S.P. - Uch. zap. Permskogo ped.
    in-ta, 1973, 113, p. 39-42.
Bolotnikov A.M., Sokolova T.I., Fufayev A.A. - In: Materialy nauch. sovesch.
    zoologov ped. in-tov. Vladimir, 1973, p. 178-180.
Bolotnikov A.M., Skryleva L.F., Zherdeva O.V. - In: The Nest Life of Birds
    (Russian). Perm, 1977, p. 3-9.
Bolotnikov A.M., Skryleva L.F., Tarasov V.A., Angalt V.Z. - Ekologiya, 1978,
    N 2, p. 86-88.
Bolotnikov A.M., Litvinov N.A., Skryleva L.F., Tarasov V.A. - In: The Nest
    Life of Birds (Russian). Perm, 1979, p. 3-11.
Bolotnikov A.M., Marks L.P. - In: The Nest Life of Birds (Russian). Perm,
    1980, p. 3-6.
Malchevsky A.S. The Nest Life of Singing Birds (Russian). L., 1959, p. 343.
Syroechkovsky E.V. - Zool. zhurn., 1975, 5, N 3,p. 408-412.
Shurakov A.I. - In: The Nest Life of Birds (Russian). Perm, 1977, p. 12-16.
Hamburger V., Hamilton H.L. - J. Morphol., 1951, 88, N 1, p. 49-92.
Parsons I. - Nature, Land., 1970, 228, p. 1221-1222.
Parsons I. The Breeding Biology of the Herring gulls (Larus argentatus).
    Ph. H.D.Thesis. Durham, 1971, p. 35-37.

PREDATION AND COLONIALITY IN SEABIRDS

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Predation is one of the driving selective forces with which all bird species must contend. Adult birds must be adapted to avoid predation on themselves and to thwart predation on their eggs and young. Virtually all predators on birds are vertebrates, but the manner of predation by the main vertebrate classes represents major ecological differences. In general predation by fish is a rare and accidental event. Reptilian predation is of major significance in the Neotropics. However, avian and mammalian predation are virtually universal hazards. The special case of human predation - whether by accident or design - will not be considered in this presentation. For a summary of the effects of human disturbance see Burger (1981a).

Various authors (e.g. Lazarus, 1972; Horn, 1968; Krebs, 1977; Ward, Zahavi, 1973), contrast protection against predation versus information exchange as the main factors selecting for avian aggregations (feeding or roosting flocks or breeding colonies). Although one might infer from published arguments that most authors (e.g., Krebs, 1977) favor a single selective factor, it is likely that both factors interact to varying degrees in determining the origin and prevalence of avian aggregations.

This paper examines the universality of predation, and the manner in which it selects for coloniality in birds, particularly coastal or marine birds. I will discuss briefly the major factors which influence predation rates. Predation must be examined by the source of predation (species of predator), the target (vulnerable birds, their eggs or their young), the mode of predation (systematic search, sudden foray), and the protective mechanisms available to the birds themselves (either passive such as habitat selection or active such as mobbing behavior).

THE SPECTRUM OF PREDATORS

Although any animal can be considered a predator with respect to its food, there is a restricted spectrum of predators that regularly consume colonial birds, their eggs or young. Predation by fish occurs away from colonies (Brooke, Wallett, 1976; Pitman, 1957). Snake predation is relatively infrequent (Lazell, Nisbet, 1972). Many species of mammals prey on colonial birds, but although evolutionary history afforded ample opportunity to develop adaptations against wild carnivores, there are many places where domestic or feral animals (e.g., dogs, cats) or human commensals (e.g., rats) represent the major threat.

Most ornithologists must, for logistic reasons, study birds relatively close to civilization. From such habitats wild carnivores have vanished,and it becomes problematic to reconstruct the kinds of predation with which colonial birds evolved. Austin (1948) summarized two decades of study in which Norway Rats (Rattus norvegicus) were the major predator on Common Terns (Sterna hirundo) in Massachusetts. However, even far from urban centers rats can be important predators as Kepler (1967) reported on Kure Atoll. Aquatic mammals (notably seals) may be important predators in certain places (Boswall,

1972). Pitman (1957) summarized reports of predation on birds at sea, mainly by seals and large fish.

Avian predators on colonial birds comprise mainly gulls and skuas, hawks and owls, herons and egrets, corvids, and frigatebirds. Avian predators can be subdivided into conspecifics (cannibals), other colonial birds (usually nesting within the colony), and predatory birds (e.g., crows, owls, hawks). Unlike carnivorous mammals, large avian predators    such as _Bubo_ sp., may persist even close to major urban centers.

Burger (this symposium) discusses the kinds and effects of predators that actually nest within seabird colonies. For our purposes, the main difference between these predators and those which enter a colony from the outside, lies in the response of the prey species. Mobbing, one the main defense mechanisms may be depressed if the predator is a bird or species, well-known to the targets because it nests in close proximity (McNicholl, 1973).

## Modes of Hunting Behavior

There have been numerous papers recently on optimal foraging strategies for predators: when, where, whom and how to hunt. Species of predators vary in the degree of stereotype of their hunting strategies. I recognize three general categories of behavior: active searching (either systematic or not), ambush, and sudden forays. Active searching is characteristic of certain herons such as Black-crowned Night Herons (_Nycticorax nycticorax_) and Cattle Egrets (_Bubulcus ibis_) that patrol beats within colonies of nesting terns. Their searching often appears to be very systematic, whereas dogs and cats appear to roam through a colony, with no predictable path. Ambush predation is seen in the case of gulls capturing fledgling alcids as they depart the breeding colony (Williams, 1975). Sudden forays are quite common, practiced by raptores and gulls and skuas alike. Such forays succeed because of their suddenness and unpredicatablity.

## VULNERABLE PHASES

Predation is not uniform throughout the life cycle. Some predators (e.g., Peregrines (_Falco peregrinus_) take adult  terns regularly, rather than eggs or young. Mink (_Mustela vison_) and owls take young terns rather than eggs, while squirrels and various shorebirds eat tern eggs, but not young. Rats and gulls, however, consume both eggs and young.

## HABITAT SELECTION AND PREDATION

Although all birds presumably excercise certain habitat preferences in choosing a nest site, evidence on nest site selection as a defense against predation is not always easy to obtain. Selection of sites such as offshore islands, cliffs, high trees, tree holes, burrows etc. that are inaccessible to predators, or sites in which predators would have difficulty locating a nest, may be the main protection against predation. Bird colonies may be placed in trees near nests of stinging Hymenopterans (e.g., some Neotropical icterids) or over water (e.g., _Quelea quelea_). Many Procellariiforms, particularly small species, nest in burrows, while cliff nesting is common in many other seabirds. Siegfried's(1977) data suggests that burrow nesting Jackass Penguins (_Spheniscus desmersus_) suffer less gull predation than surface nest-

ing pairs. The construction of penduline nests by colonial caciques (Cacicus spp.; Feekes, 1981) further discourages predation.

Although solitary nesting birds are most likely to benefit from cryptic nest placement, Tinbergen et al. (1967) showed that even in colonial species with cryptic eggs, nests would be difficult for a predator to locate, particularly if they were not placed close to one another. Tenaza (1971) found that isolated penguin nests fared worse than nests in colonies. Burger and Lesser (1978) found that salt marsh nesting Common Terns (Sterna hirundo) experienced higher predation rates for nests on mats of dead vegetation than for nests scattered among the cordgrass (Spartina patens); nests in the former habitat were much more conspicuous to human observers, hence presumably also to other predators. Nettleship (1972) and Siegel-Causey and Hunt (1981) showed differential predation influenced by habitat for puffins and cormorants, and Lemmetyinen (1973) reported that predation on tern nests varied by habitat.

## Central versus Edge Position

Coulson (1968) called attention to differences between central and edge-nesting Black-legged Kittiwakes (Rissa tridactyla). It has since been reported by many authors (e.g., Teneza, 1971; Kury, Gochfeld, 1975; Young, 1978 ),that edge-nesting birds are more vulnerable to predation. However, some avian predators may prefer to hunt in the center of colonies where the density of young is greatest, as we have seen for Harriers (Circus cyaneus) preying on Long Island's Common Terns, and as Burger and Lesser (1978) reported for gull predation rates in New Jersey terneries.

## GULLS AS PREDATORS

At the expense of ignoring such highly specialized avian predators as skuas (see Furness, 1981), space dictates that this paper consider only one type of avian predator, and I have selected gulls. Gulls are nearly ubiquitous, particularly in temperate habitats, and virtually all are colonial. Some other species, e.g., Common Terns shun gulls and will abandon traditional breeding sites after colonization by gulls. Others appear to tolerate these potentially dangerous neighbors. There is a huge literature, both anecdotal and systematic describing gull predation on many species, particularly alcids (e.g., Nettleship, 1972; Williams, 1975; Birkhead, 1977), and cormorants (Kury, Gochfeld, 1975). In many cases, gull predation is facilitated when human disturbance causes incubating birds to leave their nests unprotected (Johnson, 1938) and in some cases it appears that gulls actually follow humans into nesting colonies (Kury, Gochfeld, 1975).

Several authors have documented the proportion of overall mortality attributable to gulls. Corkhill (1973) estimated, for example, that Great Black-backed Gulls (L.marinus) took about 2% of Manx Shearwaters (Puffinus puffinus) on Skomer. Robertson (1964) found that about 12% of Australian Gannet (Morus serrator) nests were predated by Kelp Gulls (L.dominicanus) with predation particularly high on peripheral nests.

## Impact of Gull Predation on Tern Colonies

Gulls represent one of the most characteristic avian predators for nesting terns. Although gulls rarely if ever capture adult terns, they prey fre-

quently on eggs and young (Hatch, 1970). The main defensive responses of terns is to avoid areas frequented by gulls, particularly gull nesting colonies, to rely on cryptic eggs and young, and to vigorously mob intruding gulls. Not all species of terns engage in anti-predator mobbing, nor do all shun gull colonies. For example, Sandwich Terns (S. sandvicensis) regularly nest in colonies of Black-headed Gulls (L. ridibundus), and may benefit from the aggressive protection of the latter, even at the cost of losing some offspring to predatory gulls (Fuchs, 1977; Veen, 1977).

Several authors have noted that terns have withdrawn from traditional colony sites in the face of expanding gull populations. Non-migratory gulls may establish territories on former tern breeding sites, and will be incubating when the terns return from their winter quarters. Thus pre-empted, the terns seek other colony sites. Burger and Lesser (1978) have documented the decline in Common Tern nests on islands with gradually increasing Herring Gull (L. argentatus) colonies. It is apparent that as few as 10 pairs of Herring Gulls present was associated with a nearly 50% decline in a colony of 400 pairs of terns, and they found that islands with only 2 or 3 pairs of Herring Gulls experienced predation on up to 80% of the tern nests.

## Gull Predation on Other Gull Species

The size of a species is a good predictor of predatory relationships among gulls. The large white-headed species (e.g., Herring Gull) are serious threats to smaller species. Burger (1977a) provided a dramatic example of this for Barnegat Bay, New Jersey, where an increase in nesting Herring Gulls was associated with a 10-fold decline in a 5000 pair Laughing Gull (L. atricilla) colony. Laughing Gull nests adjacent to Herring Gull nests suffered 100% predation, while Laughing Gulls nesting 1 km from the larger species had less than 20% predation. In the frequent aggressive encounters, Herring Gulls won virtually all. By contrast, on Appledore Island, Maine, where Herring Gulls nest in proximity to the larger Great Black-backed Gulls, the latter species preys on young of the former and wins the majority of encounters. In both examples, it is not only that the dominant and predatory species is larger, but that it nests earlier and is ready to feed large chicks while the smaller and later species has new hatchlings. Thus, Burger found that Great Black-backed Gulls with chicks won 90 % of their encounters with Herring Gulls, while those with eggs won only 30% when they intruded on Herring Gull territories.

## Intraspecific Predation or Cannibalism

A special case of predation of paramount importance in certain species of gulls is intraspecific predation or cannibalism (e.g., Parsons, 1971; Hunt, 1975, 1976). Two modes of cannibalism can be distinguished: 1) neighbor cannibalism, where chicks are killed and often eaten when they wander onto a neighboring territory, and 2) specialist or intruder cannibalism, where certain individuals specialize on capturing young conspecifics for food. In certain other species, e.g., Common Terns, one may find chick-killing by neighbors, without actual consumption or cannibalism.

In Lesser Black-backed Gulls (Larus fuscus) Davis and Dunn (1976) reported that egg predation "usually involved a straightforward aggressive encounter

between two neighboring birds". Davis and Dunn (1976) and Hand (1981) noted that gulls that have lost their eggs or young are more likely to become cannibals, while Kirkmao (1937) believed that cannibalism of Black-headed Gulls was attributable to "unmated rogues".

Hand et al. (1981) reported that a linear arrangement of nesting territories of the Western Gull (L. occidentalis) allowed birds to reach the intertidal zone, yet return quickly to their nest if there was a threat of cannibalism. They invoke this threat as an important factor influencing the shape of gull nesting aggregations.

Thus it can be seen that the threat of cannibalism represents a substantial cost of coloniality in gulls, especially if cannibalism arises among recent victims producing a chain-reaction resulting in an increasing proportion of potential cannibals in an afflicted colony.

PREDATION SELECTION FOR COLONIAL BREEDING

A group of birds is more obvious to a potential predator than is a single individual, but although all colonial species face the potential of predation both at and away from the colony, many have chosen nesting habitats which offer essentially complete protection during the breeding season. In addition to the formation of passive aggregations in favorable habitats, there are direct benefits to nesting in colonies. A large aggregation of birds may prove more confusing to a predator (see Hamilton, 1971). Similarly the role of huge schools of fish may relate to predator confusion (Milinski, 1977).

In addition, in a large assemblage, the chance of detecting a predator early is enhanced and is spread over numerous individuals, thus allowing each individual more time to devote to feeding, maintenance behavior or parental care. Although the recognition that a flock of birds could more easily detect a predator probably occurred in antiquity, it appears to be Lack (1954) who recognized the adaptive significance of this fact for the individual within the flock. Several experimental studies (Powell, 1974; Siegfried, Underhill, 1975) showed that birds in flocks respond earlier to predators than do solitary birds; up to a point response time decreased with increasing flock size. The implications for birds in colonies are that birds feeding young can rely on neighbors to signal the approach of a predator while a group of birds can detect an approaching predator at a greater distance and fly out to meet it, thus increasing the possibility of deflecting it from the colony. These implications, however, remain as hypotheses to be demonstrated for most kinds of colonial birds.

Mobbing and other anti-predator behavior

One important benefit of coloniality is the opportunity for collective anti-predator aggression or mobbing. This has been particularly well documented for various species of terns (Lemmetyinen, 1971) and for gulls (Kruuk, 1964). It operates also for passerine birds (e.g., for thrushes, Wiklund, Andersson, 1980; for Caciques, Feekes, 1981; and for swallows, Hoogland, Sherman, 1976).

Mobbing and recognition of predators

Confronted by a predator near its nest or young, adults of many species, both colonial and solitary, engage in threat or attack behavior aimed at

thwarting the predator and driving it away. Such behavior, often accompanied by loud and characteristic vocalizations attracts other birds, both conspecifics and heterospecifics, such that the attack becomes social. Such social anti-predator aggression is widely known as mobbing.

In its own right mobbing behavior has been an important subject for ethologists because it is a high intensity, target-oriented behavior that can be predictably released (Curio, 1978). It is now documented that the target species does not mob indiscriminately, but recognizes potential predators and most of the experimental evidence is derived from species other than colony-nesting birds, even through they provide some of the most dramatic examples of mobbing. Hirsch and Bolles (1980) showed that laboratory-born Deer Mice *Peromyscus maniculatus* could distinguish between non-predators and predators from their own habitat, but not from predators that did not occur in their habitat. Curio (1978) has labelled this cultural transmission.

Common Terns react less frequently to crows or gulls that fly over a colony in swift straight flight, than in slower flight or more indirect pattern (Burger and Gochfeld unpublished). Similarly, we found experimentally that incubating Herring and Great Black-backed Gulls responded less to our approach if it were tangential rather than directly toward the nest (Burger, Gochfeld, 1981).

The effectiveness of mobbing has been mentioned in numerous anecdotes and a few detailed studies. Goransson et al. (1975) showed experimentally that large aggressive shorebirds reduced crow and gull predation on eggs set out in artificial nests. The efficacy of mobbing in protecting birds nesting in colonies has been shown for terns (Lemmetyinen, 1971), gulls (Kruuk, 1964), and swallows (Hoogland, Sherman, 1976). Burger (1981b) provides a detailed review of mobbing.

## Costs of Mobbing

Time spent mobbing a predator detracts from incubation and parental care, and may expose vulnerable young to adverse weather conditions or to predation. Emlen et al. (1966) give an example of such predator-induced aggressive parental neglect. Individuals with a high response level may spend excess time mobbing and thus show reduced reproductive success. To my knowledge, this apparent relationship remains to be tested in the field.

Mobbing also brings a bird close to a predator, increasing its own chance of being eaten (Myers, 1978). Peregrines can catch Common Terns out of a mobbing flock (Burger, unpublished observation); with practice a human can catch a mobbing Common Tern by hand, and it is likely that carnivores could accomplish this as well. This may explain why Common Terns hover over, but do not actively mob, intruding canines (Gochfeld, unpublished observation). Similarly, Patton and Southern (1978) found that gulls did not effectively mob foxes.

## Spacing and Predation

Few studies have investigated density and anti-predator behavior. Birkhead (1977) found that Common Guillemots (*Uria aalge*) in dense aggregations successfully repelled gulls; nests in sparse areas were vulnerable. Buckley and Buckley (1977) and Siegfried (1977) implicate high density nesting as a means of reducing predation on terns and penguins. Siegel-Causey and Hunt

(1981) showed lower predation on densely nesting cormorants. Density per se may be of great importance as a mechanism by which coloniality reduces relative predation rates (Gochfeld, 1980).

SYNCHRONY, COLONIALITY AND PREDATION

F.F.Darling's classic (1938) but often argued account of how gulls in colonies reduced their exposure to predation by nesting synchronously called attention to an area of both theoretical and practical interest. Elsewhere I have discussed the substance and merit of the Darling Effect in detail (Gochfeld, 1980), and here it is sufficient to mention that although several workers (e.g., MacRoberts, MacRoberts, 1972) found no evidence for the Darling Effect, other workers have found supportive evidence not only in birds (Nisbet, 1975; Williams, 1975; Birkhead, 1977; Burger, 1979b), but in fish (Dominey, 1981), and in the mast-fruiting of plants (Janzen, 1971).

CONCLUSIONS

Coloniality may reduce predation passively or actively and directly or indirectly as follows:

|  | PASSIVE | ACTIVE |
|---|---|---|
| Indirect | Many birds in safe place | .......... |
| Direct | Predator confusion | Predator detection |
|  | Dilution (safety in numbers) | Mobbing |

I have mentioned the variety of factors which influence predation. We can guess at the following quantitative relationships (see Fig. 1). Synchrony of egg-laying will have a curvilinear relation to group size. Predation is influenced by synchrony in different ways depending on whether predators are recruited. Group size may influence predation independent of synchrony. Structure of a colony, its shape and density, influence predation, as does the central or peripheral position of a nest. Mobbing behavior, itself influenced by size, density, and species composition, can be a powerful deterrent to some predators.

The challenge is to put these together into a single model. It is a challenge because the relationships between any two variables varies among species, among colonies of a single species, and even for a single colony from year to year. It is also a challenge because the interactions among variables such as colony size, density, age structure, mobbing, food availability, not to mention predator populations, makes it difficult to construct a convincing model for even one species. Developing such a model can be done on theoretical grounds or empirically, by systematic compilations of data. I favor emphasis on the latter. Even given its limitations the construction of models may facilitate gathering data in a systematic fashion.

To the extent that mobbing is important, both spatial factors (colony structure and density) and temporal factors (synchrony) are of great importance. Both within and between species there is great variation in the ways that habitat selection, predator detection, and mobbing interact, and the interactions of these factors with other features of resource use deserve investigation.

888
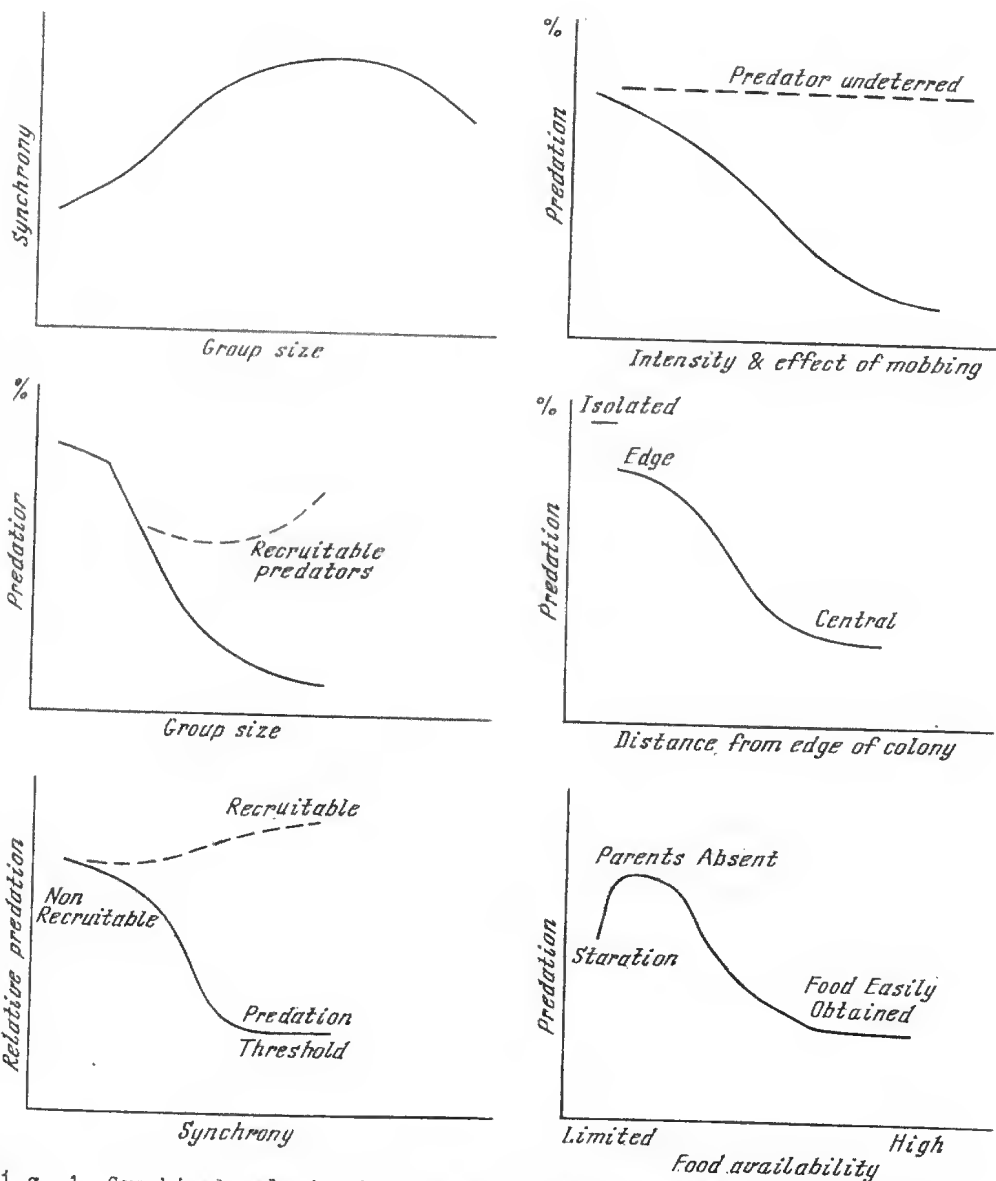
F i g. 1. Graphical relationships among variables related to reproductive synchrony and predation on colonial birds

A unitary explanation, i.e. that either food-finding or predation dictates a colonial way of life, though attractive, is unlikely to be useful. The next decade should see increasing attention to the interaction among diverse selective factors, rather than continued reliance on simplicity. I believe the time has come to respectfully retire Occam's razor.

SUMMARY

1. Predation is an omnipresent hazard faced by birds.
2. Colonies may arise as passive aggregations of individuals and species attracted to the same nesting area because it is predator-free.

3. Aggregations of birds may be more conspicuous to predators than in-
dividuals.

4. An individual's risk is diluted by being part of a large group.

5. Predators may be confused by the appearance of a dense mass of birds.

6. Birds in large groups may detect a predator earlier and need devote
less time per individual being vigilant than those in small groups.

7. In colonies, species with cryptic nests or eggs may be spaced in a
manner which thwarts the formation of an effective search-image by the pre-
dator.

8. Anti-predator aggression or mobbing is well-developed in many colonial
species, while other species may take advantage of this behavior by nesting
among the more aggressive species.

9. Anti-predator aggression is not without cost, for predators sometimes
capture the most aggressive (or least fearful) individuals.

10. The role of predation in shaping breeding aggregations in no way pre-
cludes an additive or synergistic contribution of information exchange, whe-
ther passive or active. Conversely, ones inability to demonstrate the operat-
ion of the later does not mean that in colonies birds are unable to benefit
from information conveyed by their confreres (whether conspecific or not).

R e f e r e n c e s

Austin O.L. - Bird Banding, 1948, 19, p. 60-65.
Birkhead T.R. - J. Anim. Ecol., 1977, 46, p. 751-764.
Boswall J. - Bull. Brit. Orn. Club, 1972, 92, p. 129-132.
Brooke R.K., Wallett T.S. - Ostrich, 1976, 47, p. 126.
Burger J. - Condor, 1979a, 81, p. 269-277.
Burger J. - Auk, 1979b, 96, p. 694-703.
Burger J. - Colonial Waterbirds, 1981a, 4, p. 28-36.
Burger J. - Quart. Rev. Biol., 1981b, 56, p. 143-167.
Burger J., Gochfeld M. - J. Comp. Physiol. Psychol., 1981, 95, p. 676-684.
Burger J., Lesser F. - Ibis, 1978, 120, p. 433-449.
Corkhill P. - Birt. Birds, 1973, 66, p. 136-143.
Coulson J.C. - Nature, 1968, 217, p. 478-479.
Curio E. - Science, 1978, 202, p. 899-901.
Darling F.F. Bird flocks and the breeding cycle. Cambridge, Univ. Press,1938.
Davis J.W.F., Dunn E.K. - Ibis., 1976, 118, p. 65-77.
Dominey W.J. - Nature, 1981, 290, p. 586-588.
Emlen J.T., Miller D.E., Evans R.M., Thompson D.H. - Auk, 1966, 83, p. 677-
679.
Feekes F. - Ardea, 1981, 69, p. 83-108.
Fuchs E. - Ornis Scand., 1977, 8, p. 17-32.

Furness R. - Ibis, 1981, 123, p. 534-539.

Gochfeld M. - In: Behavior of Marine Animals. Vol. 4 / Eds. J.Burger, B.Olla. N.Y.: Plenum Press, 1980, p. 207-270.

Goransson G., Karlsson J., Nilsson S.G., Ulfstrand S. - Oikos, 1975, 26, p. 117-120.

Hamilton W.D. - J. Theoret. Biol., 1971, 31, p. 295-311.

Hand J.L. - Biol. Conserv., 1980, 18, p. 59-63.

Hand J.L., Hunt G.L. Jr., Warner M. - Condor, 1981, 83, p. 193-200.

Hatch J.J. - Auk, 1970, 87, p. 244-254.

Hirsch S.M., Bolles R.C. - Z. Tierpsychol., 1980, 54, p. 71-84.

Horn H.S. - Ecology, 1968, 49, p. 682-694.

Hunt G.L. Jr., Hunt M.W. - Auk, 1975, 92, p. 270-279.

Hunt G.L. Jr., Hunt M.W. - Ecology, 1976, 57, p. 62-75.

Janzen D. - Ann. Rev. Ecol. Syst., 1971, 2, p. 465-492.

Johnson R.A. - Wilson Bull., 1938, 50, p. 161-170.

Kepler C.B. - Auk, 1967, 84, p. 426-430.

Kirkman F.B. Bird Behaviour: A Contribution Based Chiefly on a Study of the Black-headed Gull. L.: T.Nelson and Sons, Ltd., 1937.

Krebs J.R. - Natl. Audubon Soc. Res., 1977, Report 7, p. 299-314.

Kruuk H. - Behaviour Suppl., 1964, 11, p. 1-129.

Kury C.R., Gochfeld M. - Biol. Conserv., 1975, 8, p. 23-34.

Lack D. The Natural Regulation of Animal Numbers. Oxford: Clarendon Press, 1954.

Lazarus J. - Ibis, 1972, 114, p. 556-558.

Lazarus J. - Behaviour, 1979, 71, p. 127-145.

Lazell J.D. Jr., Nisbet I.C.T. - Man and Nature, 1972, 6, p. 27-29.

Lemmetyinen R. - Ornis Fennica, 1971, 48, p. 13-24.

Lemmetyinen R. - Ann. Zool. Fennici, 1973, 10, p. 526-535.

Macroberts M.H., Macroberts B.R. - Ibis, 1972, 114, p. 93-97.

McNicholl M.K. - Auk, 1973, 90, p. 92-94.

Milinski M. - Z. Tierpsychol, 1977, 45, p. 373-388.

Myers J.P. - Auk, 1978, 85, p. 419-420.

Nettleship D.N. - Ecol. Monographs, 1972, 42, p. 239-268.

Nisbet I.C.T.- Condor, 1975, 77, p. 221-226.

Patton S.R., Southern W.E. - Proc. Colon. Waterb., 1977, Group 1, p. 91-101.

Parsons J. - Brit. Birds, 1971, 64, p. 528-537.

Pitman C.R.S. - Bull. Brit. Orn. Club, 1957, 77, p. 89-97, 105-110.

Powell G.V.N. - Animal Behav., 1974, 22, p. 501-505.

Robertson C.J.R. - Notornis, 1964, 10, p. 393-403.

Siegal-Causey D., Hunt G.L. Jr. - Auk, 1981, 98, p. 522-531.

Siegfried W.R., Underhill L.G. - Animal Behav., 1975, 23, p. 504-508.

Tenaza R. - Condor, 1971, 73, p. 81-92.

Tinbergen N., Impekoven M., Franck D. - Behaviour, 1967, 28, p. 307-321.

Veen J. - Behaviour Suppl., 1977, 20, p. 1-193.

Ward P., Zahavi A. - Ibis, 1973, 115, p. 527-534.

Wiklund C.C., Andersson M. - Ibis, 1980, 122, p. 363-366.

Williams A.J. - Ornis. Scand., 1975, 6, p. 117-124.

Young E.C. - New Zealand J. Zool., 1978, 5, p. 401-416.

A NEW HYPOTHESIS  FOR THE ADAPTIVE SIGNIFICANCE OF COLONIAL
BREEDING IN THE KITTIWAKE <u>RISSA TRIDACTYLA</u> AND OTHER SEABIRDS

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Before considering the adaptive significance of colonial breeding in sea-
birds there are four general points which I wish to make concerning colonial
breeding and synchrony.

1. <u>Did colonial breeding evolve once or on several occasions</u>? The answer
to this question is that it probably has evolved several times. Not only does
it occur in almost all of the major groups of birds, the most primitive to
the most specialized, but it also occurs throughout the vertebrates being
found in fish, amphibia, reptiles, birds and in the mammals. To argue that
it evolved only once is to suggest that the evolution of the vertebrates
(and the birds) has taken place through colonial ancestors and that solitary
breeding has evolved many times as a secondary development.

If it is accepted that colonial breeding has evolved several times, there
is no reason to suppose that the same selective forces were operating on each
occasion. Thus there is no need to suppose that there is a single adaptive
significance in colonial breeding throughout the birds.

2. Once a selective pressure has brought about colonial breeding and birds
breed close together, there is opportunity for secondary adaption of colonial
breeding for other purposes. I will give a hypothetical example. Colonial
breeding may have evolved in, say, herons as a defence mechanism but further
development could then have led to social stimulation and greater synchrony
which may then be an advantage to the breeding success of individuals.

It Is Therefore Possible to Find More than One Factor which Is
Associated with Colonial Breeding which Has a Selective Value

3. It is generally assumed that synchrony of breeding is, in itself, adap-
tive, (otherwise it would not occur!). This is not necessarily so. It may be
linked to some other adaptive factor and result as a by-product. This can be
best illustrated by two examples from other animals.

a) Many insects have a quiescent stage where little or no development
takes place. This suspended development is referred to by entomologists as
diapause and its main function is to enable the insect to withstand periods
of adverse environmental conditions such as seasonal drought or low tempera-
tures. This inactivity is ended by environmental factors such as temperature
or day-length and one of the effects is that most of the individuals break
diapause and start normal development at the same time, resulting in a syn-
chronised emergence.

b) There seems to be no advantage in the varying degrees of synchrony of
breeding found in the Grey Seal (<u>Halichoerus grypus</u>) since there are no ter-
restrial predators which might prey on the pups. The degree of synchrony va-
ries geographically and occurs as a result of the environmental factors (be-
lieved to be sea-temperature) which end the suspended development of the
fertilized egg and start the normal gestation development. The rise in sea
temperature is more rapid in certain areas and this causes greater synchro-
ny of implantation and hence births amongst the cows. Here the primary adap-
892

tive value is to adjust the breeding season to an annual one; the synchrony is secondary (Coulson, 1981).

4. It is worth considering how difficult it would be for a bird species to eliminate colonial breeding if it was no longer an advantage. It should not be assumed that the evolution from solitary to colonial breeding is as easy to achieve in the reverse direction. First of all, many colonial breeding birds have given up the ability to breed as one male and one female in isolation. A further component is necessary to bring about successful breeding in many species; that is the stimulation of other individuals. Having become dependent on other individuals how easy is it to loss this dependence? It should be remembered that the evolution from situation B to A may be much more difficult than the evolution from A to B. Many free living species have evolved into endoparasitic species; few if any endoparasitic species have become free living.

Whilst I do not subscribe strongly to the view that in some species colonial breeding may be no longer an advantage; consideration should be given to this possibility occurring in some species.

THE ADAPTIVE SIGNIFICANCE OF COLONIAL BREEDING

In this paper, I present a new hypothesis to explain the function and adaptive significance of colonial breeding in birds. The hypothesis does not claim any function in colonial breeding which may not be found in solitary breeding species. It merely considers that colonial breeding achieves more effective adjustment of the breeding season to the time which is optimal for young production. This is of particular importance in species which breed in climatic regions where the environmental conditions and, presumably, the time for optimal breeding success vary from year to year. This adjustment is also of value to individuals which may not be as 'fit' as others and cannot afford to invest as much in breeding, or for example, if the individuals trade off survival against reproductive success in a particular year.

The simplest explanation of the ability of a species to adjust its breeding season to varying environmental conditions is that there are two rates of development towards full reproductive condition in the period leading up to egg laying; the slower rate operating in adverse conditions and the faster rate when conditions are favourable. Otherwise breeding would take place at the same time each year. I suggest that there are two rates of development towards reproductive condition in colonial birds; one when the birds are away from the breeding colony and the other when they are paired, living for much of the time in the colony and are subject to social stimulation from their neighbours. The time of return to the colony is both a good measure of the reproductive potential of an individual and an indication of whether the conditions leading up to the breeding season favour early or late breeding.

I have built the model around the Kittiwake <u>Rissa tridactyla</u> but the important factors in this species, return to the colony being related to laying date and breeding success being higher in early breeding individuals, are, from my own experience, characteristic of many seabird species, particularly the Shag <u>Phalacrocorax aristotelis</u> and the Herring Gull <u>Larus argentatus</u>.
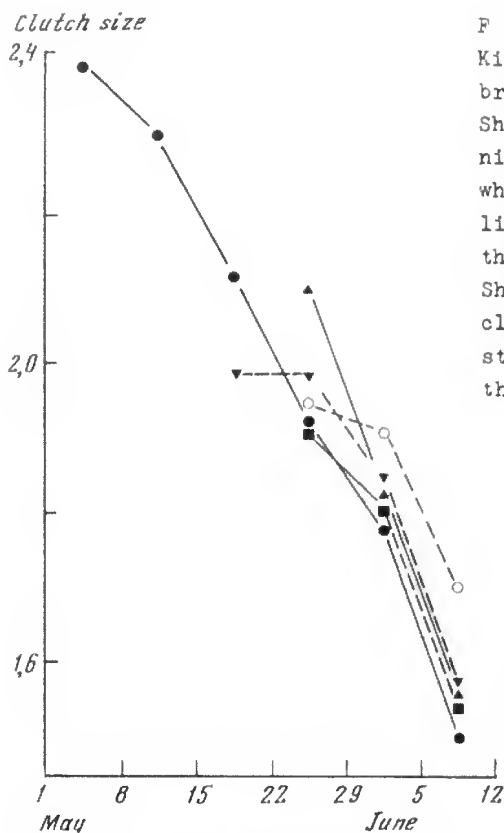
F i g. 1. Clutch size variation in the Kittiwake *Rissa tridactyla* through the breeding season. Data from the North Shields colony and four other colonies in eastern Britain. Note that whilst in all colonies clutch size declines as the breeding season progresses, the colonies starting later than North Shields do not lay as large average clutch sizes early in the season but start laying at that appropriate to the actual date

Many **seabirds**, particularly those which breed in the Arctic, show considerable variation in breeding dates from year to year. This variation has been documented for several species by Belopolskii (1957) who shows, for exampls in the Kittiwake, than in four consecutive breeding seasons (1947-50) first laying varied by 18 days in eastern Murman. In contrast, the same species shows much less variation in Britain. Clutch size varies with the early or late breeding. Belopolskii (1957) has recorded a mean clutch size of 2.33 in an early year and 1.53 eggs in a late breeding season. In fact the Kittiwake shows a remarkably consistent pattern of clutch size change with date. Fig. 1 shows the data for my study colony at North Shields (dots and continuous line) and that in other (later), breeding colonies in eastern Britain. Note that later breeding birds lay a lower clutch size in the same colony and also that the individuals in later breeding colonies lay clutches appropriate to actual date and not to their relative date for the colony (Coulson, White, 1961). Thus late breeding produces small clutches and this is obviously the same throughout its range. The examination of clutch size variation in the same female breeding in successivs years has also revealed that there is a strong tendency for clutch size to be lower when breeding is late.

Clutch size is a good indication of breeding success in the Kittiwake. Table 1 shows the breeding success in relation to clutch size; the larger the clutch, the greater the number of young fledged and clutches of three eggs havs almost the same percentage success and the normal clutch of two

T a b l e  1. Breeding success in Kittiwakes at North Shields, England, 1954-1979 based on 1406 clutches

| Clutch size | Breeding success % | Young fledged per pair |
|---|---|---|
| 1 | 40.0 | 0.40 |
| 2 | 62.0 | 1.24 |
| 3 | 60.7 | 1.82 |

eggs. The seasonal variation in breeding success is shown in Fig. 2. Apart from a suggestion of slightly lower success in the earliest breeders, the later breeding birds have a lower breeding success (mainly as a result of the lower clutch size laid by these late birds). Clearly early breeding Kittiwakes are more productive breeders.

Early laying Kittiwakes are, in general, also the birds which return to the colony early. The relationship between date of return and egg laying for individual birds (data grouped) are shown in Fig. 3. In my study colony, where some birds return as early as January, early return results in early breeding but the sxact date of return has little effect until the end of February, after which time the later the birds arrive, the later egg laying oc-
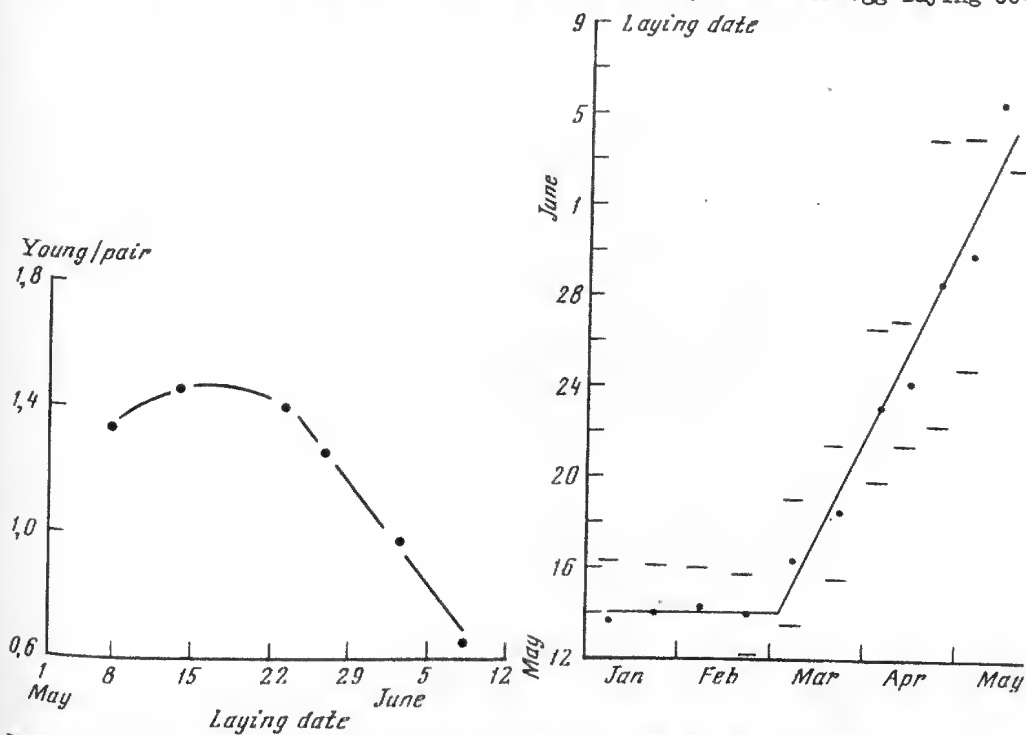


F i g. 2. The breeding success of Kittiwakes Rissa tridactyla through the breeding season. Data from the North Shields colony

F i g. 3. The relationship between the date of return to the colony and the date of laying the first egg of the clutch for Kittiwakes Rissa tridactyla breeding at North Shields. The bars show the 95% confidence limits for each point
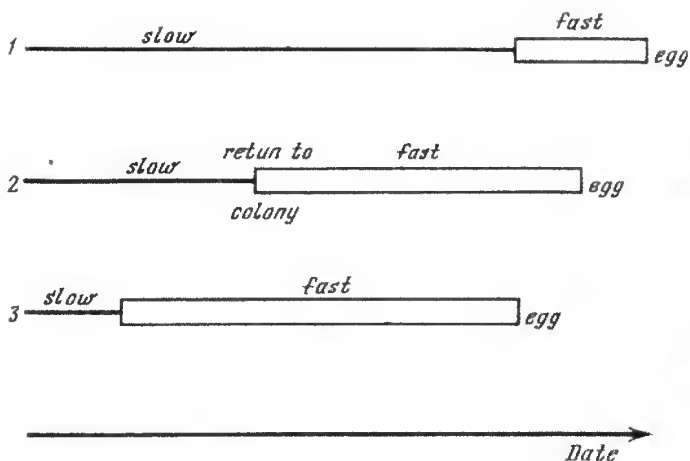
F i g. 4. Three examples of the relationship between the onset of development towards reproductive condition, date of return to the colony and the date of egg laying interpreted with slow and fast rates of development

curs. (Note that return in March is typical of most Arctic and sub-Arctic Kittiwake colonies).

It is possible to interpret the situation operating from March as indicating that there are two different rates of development towards breeding condition; one in those which are solitary and another in those which are colonial. Fig. 4 illustrates the situation with 3 examples. It is an easy task to calculate the relative rates of development in the two situations, by using the relationship:

(days) (slow rate) + (days ) (fast rate) = development to egg laying.
Taking two different birds, ths left sides can be equated and the ratio $\frac{\text{fast rate}}{\text{slow rate}}$ can be determined as 1.22, that is ths fast rate of development takes place 22% fastsr in the colony.

Fig. 5 shows the relationship between the duration of the pre-egg stage in the colony and the laying date in the Kittiwake (using the data from Fig. 3). As the time of laying becomes later in the season, the period of time needed in the colony becomes less (that is, less social stimulation is needed).This also indicates that dsvelopment is taking place when the birds are oceanic and have not yst returned to the colony, as wsll as implying that more social stimulation from the colony is necessary if breeding is to be early. Of interest is the point where breeding would occur without rsturning to the colony (although the bird would obviously need a mate). The date, about 10 June, is the time of cessation of egg laying in Britain. At this time an environmental induced barrier to later egg laying (including replacement clutches) occurs. It is possible that ths combination of the slower development of reproductive condition in solitary birds and the seasonal termination of egg laying prevent Kittiwakes from breeding as isolated pairs.

Changing from a slow to a faster rate of development towards breeding has two further effects on the pattern of laying in the colony. First, the increase in the rate of reproductive development results in increasing synchrony. This is a general effect found in any biological system where the rates of development increase. Secondly, the change over from the slower to the faster rate at different times in individuals results in skewing the brsed-

896
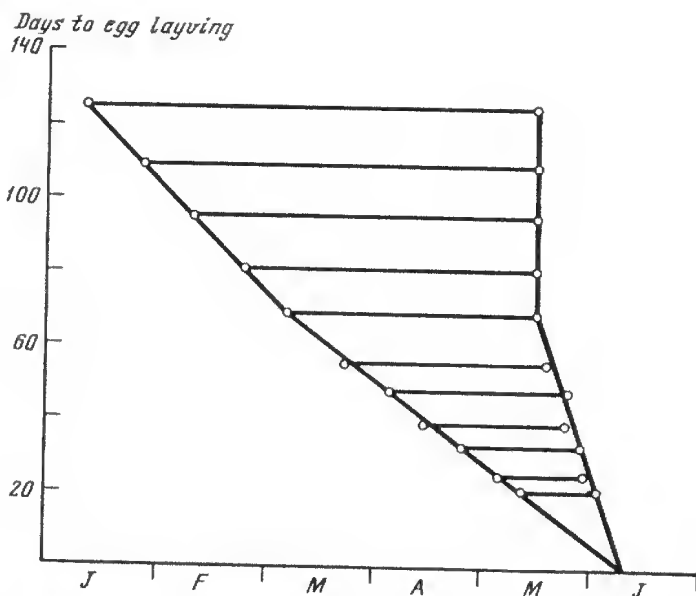
F i g. 5. The relationship between date of return to the colony and the date of laying. Note: (i) the shorter period of presence in the colony of late arriving birds before egg laying, and (ii) the date (about 10 June) when, in theory, Kittiwakes should be able to lay without being colonial. In practice, egg laying is inhibited about this date
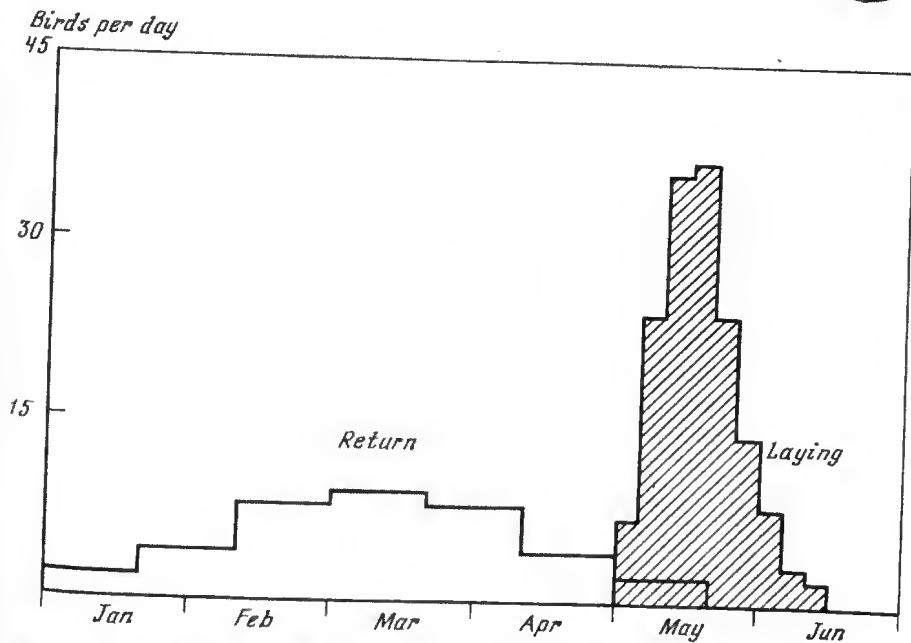


F i g. 6. The effects of slow and fast development rates towards breeding condition on the shape of the breeding season. The change in rate produces an asymmetrical breeding season with a tail of late breeding although the dates of return were symmetrical

ing season. I have illustrated this in Fig. 6 by taking a symmetrical, near normal distribution of the time of return (corresponding to the actual situation). By applying the development rates before and after the time of return the skewed distribution of breeding, with a tail of later breeder is obtained. Gochfeld (1980) has drawn attention to this typical asymmetrical pattern in seabirds and in 27 out of 28 cases examined, a skew with a tail of late breeding was found. He did not offer any explanation of this distribution. It is possible that all of these patterns stem from the change in rate of development towards breeding condition occurring at different times in different individuals.

## ADAPTIVE SIGNIFICANCE

The more precisely an individual can adjust its breeding date to optimize its reproductive output, the greater the selective advantage. I doubt if any species can achieve this precisely; perfect adaptation does not exist. I suggest, however, that colonial breeding may achieve this to a greater extent than the methods used by solitary breeding birds. The group stimulation or social stimulation (Darling, 1938) is an essential part of this concept and there is clear evidence· of it occurring in the Kittiwake (Coulson, White, 1960; Coulson, Dixon, 1979). I may have simplified the concept in referring to two different rates of development towards breeding condition, the social stimulation effects will vary between birds nesting at different densities. However this will put only a small range on mean of 22% increased development under colonial conditions, perhaps from 15% to 30%.

The prime function of the stimulation between the members of the pair and, in colonial species, between neighbouring birds, is to complete reproductive development and initiate egg laying at a time which, as far as possible, maximizes young production (or more correctly, young which survive to adulthood). The greater the ability of individuals of a species to adjust the breeding season, the greater the probability of higher young production, which is, of course, a considerable selective advantage. In many seabird species, the earlier breeders are more successful, but this is only after the birds have adjusted their breeding date in response to environmental clues. If birds bred as early in years when conditions are unfavourable as they do in other years. I suspect these early breeders would have a very low success. I believe that adjustment of the breeding season is more important than synchrony between members of a colony. Having said this, I wish to emphasise that this does mean that, in some species, synchrony may itself be a selective advantage.

This model moves from concepts which are unique to colonial birds. It also has the advantage of explaining anomalies in other concepts or unexplained effects in colonial breeding. There is no longer the difficult problem of greater spread in larger or denser Kittiwake colonies where the selective advantage in synchrony fall down. Synchrony is a by-product of this hypothesis. If it can be adapted to the advantage of the species, as for example Parsons (1975) has shown beautifully for the Herring Gull, then the species obtains a bonus benefit; this is a secondary advantage but it does not have to occur in all species. In the Kittiwake, the synchrony is

in small groups within the colony (Coulson, Dixon, 1979); groups which are too small to obtain benefit from swamping a predator with food.

Further the model explains the asymmetry of the breeding season in many seabirds . It also has the merit that it does not propose a new function but merely suggests that colonial birds can adjust their breeding season to their advantage better than solitary breeders. This last point is one which could be examined to test the hypothesis. Are colonial breeders better able to adjust their breeding season than non-colonial birds in the same area? Presumably this would be expected to manifest itself by greater variation in date of laying between years in colonial species.

SUMMARY

The paper starts with four generalizations about colonial breeding:

1. Colonial breeding has evolved on several occasions.

2. Once colonial breeding is established in a species other, secondary selective advantages can evolve so that there could be more than one selective advantage found when investigating the advantage of group breeding.

3. It is often assumed that synchrony of breeding is always adaptive. This need not be so; it could arise from being the by-product of some other adaptive factor.

4. It could be very difficult for a species which has evolved colonial breeding, but which is now no longer adaptive, to eliminate this behaviour and return to breeding as solitary pairs.

It is suggested that the adaptive value in colonial breeding lies in possessing two different rates of development towards egg laying. A slow rate occurring when solitary and a faster rate when the birds are in the colony. This allows adjustment of the breeding season to a time which maximises breeding success under the prevailing conditions. A by-product of this is 1) synchrony of breeding and 2) a skewed breeding season with a tail of late breeders. Both of these are well known in seabirds . The model is illustrated by the breeding biology of <u>Rissa tridactyla</u>.

R e f e r e n c e s

Belopolskii L.O. - Ecology of colonial sea birds of the Barents Sea. Moscow; Leningrad: AN SSSR Press, 1957.

Coulson J.C. - J. Zool. Lond., 1981, 194, p. 553-571.

Coulson J.C., Dixon F. - In: Biology and Systematics of Colonial Organisms/ Eds. G.Larwood, B.R.Rosen. L.: Acad. Press, 1979, p. 445-458.

Coulson J.C., White E. - Ibis, 1960, 102, p. 71-86.

Coulson J.C., White E. An analysis of the factors influencing the clutch size of the Kittiwake, 1961.

Darling F.F. - Bird Flocks and the Breeding Cycle. Cambridge University Press. Cambridge, 1938.

Gochfeld M. - In: Behaviour of Marine Animals Vol. 4. Marine Birds / Eds. J.Burger, B.L.Olla, H.E.Winn. N.Y.; L.: Plenum Press, 1980.

Parsons J. - J. Animal Ecology, 1975, 44, p. 553-573.

# EVOLUTION OF SOCIABILITY, FORMATION AND STRUCTURE OF MONOSPECIFIC AND MIXED COLONIES OF SPARROWS FROM THE SUBFAMILY PASSERINAE

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Ornithologists traditionally show great interest in the family Ploceidae, and unparalleled diversity of social relationships within this group is being one of that reasons. Many weavers and sparrows are known to nest in colonies, some comprising as many as hundreds of thousands of pairs and other consisting of no more than a few dozen birds. Representing the third type of colonies, there are in fact none other than amorphous gatherings of pairs. At last, some species nest in isolated pairs. Any multispecies genus of the family is characterized by a whole range of spacial relations between its member-species, the key problem being how to account for this diversity.

We have studied representatives of the genera Passer, Petronia, Pyrgilauda, Carpospiza, and Montifringilla. All of them are endemic to the Asiatic continent, exclusive of genus Passer occurring both in Africa and Asia. These genera are often incorporated into the subfamily Passerinae.

This sub-family features a total range of behavioural patterns, from genuine territorial to highly developed obligatory colonial spacing.

Thus occupation of the burrows of rodents by isolated pairs is the only form of nesting for the Pere David's snow finch inhabiting the relatively flat mountain steppes. Nests are usually spaced at no less than 80-100 metres even in undisrupted populations of this species, their high density and abundant nesting space not withstanding.

Snow finches, found in rugged highland, prefer solitary nesting although groups of 3-4 nests separated by 8 to 10 metres, are sometimes found.

It is noteworthy that genuine display flights are inherent in both snow and Pere David's snow finches just as in many other species with territorial behaviour.

The breeding season being over, both these species form large sometimes mixed flocks and turn to nomadic way of life.

Pale rock sparrows, inhabiting foothill semideserts, form pairs that nest separately and, as observed by Adamyan (1965), also keep their territories actively guarded.

Spacial structure of the rock sparrow settlements is highly variable. Most are incompact groups of 5 to 12 males, displaying shelters for the nests to be placed at a distance of 10-15 metres. Once the pair is formed and the female gets to nest-building, the male occupies another shelter, starting to display it until a new mate is gained. The settlement density is thus growing significantly. Side by side with such amorphous colonies there are lone males whose number can amount to about 30 per cent of the population. Our observations have not revealed any relationship between the time when a male gains its first female and his social environment.

Apart from nesting seasons, rock sparrows live in large flocks numbering scores of birds. They can also form transitory flocks of 4 to 8 individuals when foraging during breeding periods.

The genus _Passer_ also includes both territorial and highly colonial species.

The saxaul sparrow was observed to defend its territory within a range of 40 to 50 metres. Neighbouring territories are often widely overlapping. Protracted border conflicts, involving both males and females, are a common occurrence in the areas shared by two or more pairs. The pair makes the most of the whole of its territory, and social contacts between the partners take place all over it, being not confined to the immediate vicinity of the nest. All the shelters suitable for placing nests within the individual territory: nest boxes and other types of artificial shelters, are defended from other conspecifics. E.I.Gavrilov has reported cases of polygyny in the saxaul sparrow.

The species forms flocks in winter and during migrations. In spring the birds of migratory flights were observed to inspect closely situated nest-boxes while their owners were away. These birds were apt at forming a sort of colony, but on returning the holders of the territory immediately drove away all the intruders. Thus the saxaul sparrow is likely to set up small colonies, provided that birds simultaneously move into neighbouring hollows.

Spacial structure of the tree sparrow settlements looks very much like that of the rock sparrow. Tree sparrows are most often seen to form solitary pairs and sometimes sparse gatherings, with nests spaced at 6 to 8 metres.

Colonies of the house sparrow are by far more compact as compared to those of the tree sparrow.

Colonies of Spanish and Indian sparrows are known to number tens or hundreds of thousands of pairs, the nests being set so close to each other as to fuse into conglomerations. The Spanish sparrow places nests on trees only, while the Indian sparrow uses cliffs and rocks as well.

As regards the spacial structure of the colonies of these species, both of them are apt at defending a limited area around the nest. Its size depends to a large extent on the synchrony of moving into a given section of the territory. Peculiar nest-clusters are usually formed in case of simultaneous settlement. Members of these settlements are very tolerant to one another but any intruders are immediately driven away. In cases of asynchronous installation the density of the colony is much lower.

The male of Indian sparrow occupies a portion of a tree crown up to 50 cubic metres, with one or more forked branches suitable for nest disposition. The whole of the territory is continually patrolled and inspected. Border conflicts with neighbouring males are of frequent occurrence, lasting a few minutes and accompanied by characteristic displays.

The male of Spanish sparrow occupies but one fork, immediately laying the basis of its would-be nest. It spends all his time in the nest or hereabout, paying no attention to what is going on in the closest proximity. Border conflicts in this species are non-existent, all agonistic relations being reduced to short-term contacts. Nevertheless the nest is said to be defended.

Colonies of Spanish sparrows are generally characterized by greater density than those of Indian sparrows. New groups of Spanish sparrows, numbering 6 to 10 males, may often move into already established colonies. They arrive in a compact flock, each bird occupying its own fork close to one another and setting in singing or displaying. Then they proceed to nest-building

stealing nesting materials from and one another and weaving their individual constructions together into a single conglomerate. The latter is never formed in case of asynchronous installation.

The Indian sparrow is often observed to nest in solitary pairs or small colonies of 5 to 10 pairs. Isolated colonies of Spanish sparrows never have less than 30 to 40 pairs.

Mixed colonies of Indian and Spanish sparrows on threes are most common. Rock and Indian sparrows usually form mixed colonies in urban areas while tree and Indian sparrows place their nest under house-tops in rural localitites.

In mixed colonies member-pairs guard their own nesting sites against any passering species. Yet those claiming for a shelter occupied by a pair of different species may turn out to be very persistent, employing it while its owners are away for foraging.

Indian sparrows are known to occupy the Spanish sparrows' nests already 3-4 days before they are abandoned by nestlings. At first the parents display a highly aggressive behaviour, while subsequently they get used to the intruders and do not prevent them from penetrating into the nests and feeding the young. Pairs of Indian sparrows are often formed in such circumstances.

We have found a few cases of interspecific stimulation of reproductive behaviour in mixed colonies. Indian sparrows, arriving rather late, are seen to form colonies first of all where resident tree and rock sparrows can be found. Odd males of both these species first and foremost attract Indian sparrows because of their ceaseless singing. The earlier nesting of Indian sparrows is observed in such mixed colonies. Another example is that of the Spanish sparrow which may form solitary nesting pairs or groups of 5 to 7 pairs within large colonies of Indian sparrows.

Having now accomplished the survey of structural patterns of social systems in representatives of the subfamily Passerinae, we proceed to the analysis of some functional aspects of colonial nesting in Indian and Spanish sparrows.

Both species arrive at the breeding ground rather late. When outside the colony during this initial period, they form compact flights and are characterized by highly synchronous comforting, foraging, defensive, and locomotor behaviour. Their nuptial, aggressive, and territorial behaviour can already be clearly seen when the birds are still in migratory flocks. Bouts of their social activity are also highly synchronized. They are most manifest when the birds are gathering at roosts in the evenings or before they leave for foraging early in the morning. The nesting colony is often formed in such places of roosting.

The flock-size is highly variable. Thousands of birds can be brought together in spring on agricultural lands with prevalent grain farming. They are foraging in the fields but never far from trees, serving as resting places, shelters from predators, and roosts. Large flocks in excess of 40 to 50 birds are not formed outside agrocenoces.

Colony territories are being settled gradually, in a sort of cyclic pattern. Such patterns of behaviour are particularly manifest in Indian sparrows, nesting on rocks or cliffs.

During the first few days after arrival Indian sparrows can be seen at the colony but for a short time in the morning. For the rest of the day small dense flocks of them are foraging in its vicinity. The birds often roost on trees rather far from the would-be colony site. Later on they begin visiting the colony in the evenings, and their roosting sites are brought as close to it as possible. At last morning stay in the colony becomes even longer, and the birds can be seen there in the afternoon. There are always birds in the colony after nest-building begins. The first eggs having been laid, females roost in their nests while males spend the whole of the lighttime in the colony, leaving it only for the night to roost on the nearby trees.

The flock size in the foraging habitats is consideralby reduced by this time. Synchronous behaviour is lacking, bird gatherings are but transient.

When near the cliff to be chosen as a nesting site, some birds usually occupy it while others can be seen on the nearest tree. There are all kinds of social interactions between members of both groups, accompanied by continuous interchange of birds between the two places. Birds move in groups of 5-6 individuals in a highly synchronized way. As the colony is being formed, the birds spend more and more time on its territory, their antagonistic relations becoming, more and more pronounced. Sparrows move in and out of the colony alone irrespective of actions of other conspecifics. Trees are used only for roosting or in case of flushing synchronously when they leave the cliff being stricken by the so-called "false panic" or getting sight of a predator.

In the majority of cases such flushes are supposed to occur spontaneously, they happen however, far more often if predators are constantly present. The frequency of such spontaneous flushes decreases anyway as the birds' attachment to the colony grows until they cease to be seen at all when nest-building is started. There is significant negative correlation between flush prevalence in different, even if adjoining parts of the colony, and the duration of the birds' permanent stay in them. Flush prevalence positively correlates with the population density in a given section.

We compared two types of Indian sparrow nests to elucidate the effect of the population density on bird behaviour. Some nests were placed in the middle of the colony, no more than 30 cm apart from each other. The rest of them occupied peripheral portions of the colony, separated from other nests by no less than 2 metres. Male holders of the centrally located nests were observed within an hour to mate, participate in agonistic contacts with other birds, and be involved in flushing in company with their neighbours 1.5; 4 and 2.3 times as often as owners of the peripheral nests respectively.

Energy consumption for flushing is the greatest. About a hundred flushes per day can be seen at the outset of colony formation, each lasting for 8 to 10 seconds. This makes up 15 minutes, enough for a bird to cover a distance of 10 kilometres. This energy consumption rate is said to be comparable to that required for locomotor activity exhibited by foraging birds during this period.

Increased exitability is known to develop in birds inhabiting densely populated parts of the colony, due to their numerous social contacts. It has been established by irritating birds with sunbeams, caught in a mirror and

serving as a potent discomfort factor. Only 36 per cent of affected birds occupying densely populated sites could stay put for more than a minute. All others flew away much quicker. 73 per cent of males in the sparsely populated portions of the colony endured a one-minute irritation by sunbeams.

The pressure of predation on a sparrow colony often results in disastrous effects. Hawks and small falcons can be seen in a colony all day long, catching both adults and fledglings. Snakes, magpies, jackdaws, and even shrikes are known to prey on eggs and nestlings. Unable to defend their nests from predators, sparrows can do little more than to try and scare them away with yells. It is interesting that birds get used very soon to the permanent presence of predators, especially in large colonies.

Breeding success is far from being equal in different colonies, largely depending on the influence of predators. Jackdaw invasions are fraught with the most disastrous consequences. T.F.Pedyanina has shown that they are able to exterminate up to 65 per cent of nestlings. Meanwhile, predators being absent, practically all nests give rise to fledglings. Thus nesting success is largely dependent on incidental factors.

We have studied breeding success in Indian sparrows, nesting in the holes of a cliff, using incidence of hatching failure as an indicator. Examination of nest contents was impossible by force of circumstances, and we could not wait for the fledglings to leave the holes. We therefore considered successful pairs that proceeded to feeding nestlings. In all, 67 and 48 nests were under observation in the densely and sparsely populated portions of the colony respectively. In the former case 18 nests were unsuccessful while only 4 in the latter, with jackdaws being the main predators.

In case of arboreal nesting, densely populated sites were observed to be most attractive for predators as well.

I am afraid that the data reported would seen disappointing in terms of adaptive significance of bird colonies. In fact, the greater their size and density the more attractive they appear to be for predators. Moreover, constant excitation of birds, resulting from a great number of their social contacts considerably increases energy consumption. At last, birds have in forage as far as 1.5 kilometres away from the colony.

Nevertheless this is exactly the way with colonial sparrows, making the validity of hypotheses of the advantages of colonial nesting open to question. Even if this is the case, a species is certain to pay dearly for such advantages. One unavoidably arrives at the conclusion that a social system, based on obligatory colonial bonding, can be functionally efficient only within a relatively narrow range of favourable ecological conditions.

# ADVANTAGES AND DISADVANTAGES OF MIXED-SPECIES COLONIES OF SEABIRDS

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## INTRODUCTION

The disperson of nesting birds varies from species that nest solitarily to those that nest in densely-packed groups of thousands of individuals. The nesting pattern for species is a continuum from solitary nesting to dense groups. Thus it is difficult to define a colony, although definition is essential to understanding the biology of seabirds. I define colonies as comprised of birds that nest in close proximity to one another, interact regularly, and use their territories only for breeding activities.

Seabird colony sites are usually on coastal or marine islands, and suitable nest sites are often limited, forcing many species to nest together (Belopol'skii, 1957; Bianki, 1977; Bergman, 1980). The spatial overlap of seabirds is often difficult to determine. Many seabird publications do not indicate whether other species nest nearby or on the same island; or if nests of various species are intermingled. Several authors mention that different species nest in mixed-species groups, and give numbers of nests or maps showing the locations of nests (i.e. Brun, 1976; Amerson, Shelton, 1976; Furness, 1981). Such studies can be used to examine the extent to which seabirds nest in mixed-species colonies (colony where birds nest next to heterospecifics). Whether species separate into monospecific clusters is often impossible to ascertain, although intermixed nesting often occurs in members of the same family (i.e. gulls, penguins). Even when nests are mixed interspecifically, clusters of monospecifics may be evident. On Johnston Atoll nine species nest intermixed, but each species clumpes monospecifically (Amerson, Shelton, 1976; Table 1).

Seabirds frequently form mixed-species colonies, particularly on isolated marine islands. Such groups may be the rule rather than the exception (Belopol'skii, 1957), and some species of most sympatric seabird families sometimes nest together in mixed-species colonies (Table 2). Exceptions occur with pelicans, darters and skimmers, usually inland nesters in colonies with conspecifics, larids, or ardeids. Seabirds frequently nest in colonies with non-seabirds: gulls, terns cormorants and anhingas nest with ardeids (Ellison, Cleary, 1978; Morrison et al., 1979; Burger, 1981). In this paper I discuss the benefits and costs of mixed-species seabirds colonies.

## ADVANTAGES AND DISADVANTAGES OF MIXED-SPECIES COLONIES

The disadvantages of mixed-species colonies result from competition for food, space and nesting materials, disease transmission, piracy and predation; while the advantages result from improved predator detection and protection, information transfer, reduced competition for space, nest materials and food, and social facilitation. Although these factors operate in monospecific colonies (see Burger, 1981), their relative importances differ in mixed species colonies.

Table 1. Dispersion of Groups of Nesting Seabirds on Johnston Atoll (after Amerson, Shelton, 1976)

| | Number of Groups | Percent Occurrence | Percent of Conspecific as Nearest Groups |
|---|---|---|---|
| Ground-nesting species[a] | | | |
| Wedge-tailed Shearwater | 163 | 54 | 90 |
| Christmas Shearwater | 4 | 1 | 0 |
| Red-tailed Tropic bird | 2 | <1 | 0 |
| Brown Booby | 14 | 5 | 43 |
| Brown Noddy | 117 | 39 | 93 |
| Gray-backed Tern | 2 | <1 | 0 |
| Tree-nesting species[b] | | | |
| Red-footed Booby | 5 | 22 | 100 |
| Great Frigatebird | 13 | 56 | 85 |
| Black Noddy | 5 | 22 | 100 |

[a] Goodness of Fit $\underline{X}^2$ = 125.1, df = 4, P < .001
[b] Goodness of Fit $\underline{X}^2$ = 35.6, df = 2, P < .001

## Resource Utilization

Space: Individuals nesting in a colony where optimal sites are in short supply compete for nest sites. In theory, competition among species for sites is less than within a species, but direct tests of competition among species are rare. For several seabirds, nest site differences have been noted. In the South Orkney and South Shetland Islands, penguins use different nest sites: Adelies nest at higher elevations, Chinstraps nest in sloped areas, and Gentoos nest on flatter areas (White, Conroy, 1975). Similarly, Rock-hopper and Erect-crested Penguins on Antipodes Island nest in slightly different habitats (Warham, 1972). Nest site differences have also been noted in Albatrosses: on Midway Atoll Black-footed Albatross prefer open sandy areas near the sea whereas Laysan Albatross use sheltered areas with some vegetation (Frings, Frings, 1961). On Marion Island, however, Berruti (1979) suggested that Sooty and Light-mantled Albatross use different habitats, but interspecific competition could limit the nesting of Light-mantled Albatross. Warham et al. (1977) describes differences in nest sites selected by several species of shearwaters, petrels and diving petrels on the Snares Islands, and Harris (1969) noted that there was little competition for nest sites between Shearwaters and Madeiran Storm Petrels on the Galapagos Islands. Great and Lesser Frigatebirds on Aldabra Atoll use different nest sites, but there is some overlap (Diamond, 1975a). Herring and Lesser Black-backed Gulls nest together in Kandalaksha Bay with no competition as Herring Gulls nest on bare rock outcroppings and Lesser Black-backed Gulls nest in vegetated areas (Bianki, 1977). Harris (1963) reported similar differences among these species on Skomer Island. Rhinoceros Auklets, Pigeon Guillemots and Tufted Puf-

Table 2. Members of these families seabirds that nest with members of other seabird families. Above the diagonal shows whether they nest in mixed species colonies (X), or do not overlap in breeding range (O). Below diagonal shows references for those relationships (letters refer to literature cited)

| | Penguins | Albatrosses | Petrels | Storm Petrels | Diving Petrels | Tropic birds | Pelicans | Gannets Boobies | Cormorants | Darters | Frigatebirds | Skuas | Gulls Terns | Skimmers | Alcids |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Penguins | – | X | X | X | X | | | | X | | | X | X | | |
| Albatrosses | | – | X | X | X | | | X | X | | X | X | X | | |
| Petrels | 30,65 | 13,48 | – | X | X | X | X | X | X | | X | X | X | X | X |
| Storm Petrels | 65 | 2 | 26,48 | – | X | X | X | X | | | X | X | X | | X |
| Diving Petrels | 65 | | 26,62,65 | 68 | – | | X | X | X | | X | X | | | X |
| Tropic birds | | | 26 | | | – | | X | X | | X | X | | | |
| Pelicans | | | 26 | 26 | | | – | X | X | | X | | X | | X |
| Gannets | | 2,12,33,34 | 2 | 2 | | 1,2 | | – | X | | X | | X | | X |
| Boobies | | | 2 | 2 | | | | – | X | | X | | X | | X |
| Cormorants | 35,50,65 | | 14 | | 28 | | 3,51 | 2,43,59 | – | X | X | X | X | | X |
| Darters | | | | | | | | | | – | – | | | | |
| Frigatebirds | | 12 | 2 | 2 | | 2 | | | 11 | – | – | X | X | | |
| Skuas | 32,64,67 | | 2 | 2 | 68 | 24 | | | 36 | | 24 | – | X | – | X |
| Gulls Terns | 65 | | 68 | 24,40 | 68 | | | | | | | 25,69 | – | X | X |
| Skimmers | | | 28 | | | | 31 | | | | | – | 10,20,52 | – | – |
| Alcids | | | 28 | 28 | | | | | | | | | 6,29,44,55 | – | – |
| Monospecific | 32 | 27,45,56 | 24 | 7,37,44,55 | 35 | 35 | 35,42 | 8 | 18,19,55 | 41 | 1,5 | 52,67 | 24,35 | | 21,38,49 |
| Monofamilic | 60,61,65 | 2,13 | 57,62,65 | 4,23 | 54 | 54 | | 36 | 36 | 36 | 16 | 22 | 39 | | 59,63,5,6 |

fins on Protection Island (Washington) also showed specific nest site diffe-
rences (Richardson, 1961). Similarly, Grant and Nettleship (1971) reported
that Fulmars and Puffins nesting on cliffs do not restrict nest site selec-
tion of the other species.

In these cases each species used different parts of the habitat, and in-
terspecific competition was not reported. However, habitat distribution does
not always follow directly from habitat preference. Intra- and interspecific
competition may exclude birds from their preferred habitats. For example, in
some areas Red-tailed Tropic birds and White-tailed Tropic birds had only a
6% overlap in nest site types (Prys-Jones, Peet, 1980), but Diamond (1975b)
reported a 78% overlap on Aldabra Atoll, suggesting intense competition. On
Ascension Island, Red-billed and White-tailed Tropic birds competed for nest
sites, and the ownership of nest sites changed frequently (Stonehouse, 1962).

Interspecific competition for nest sites can result in nest take-overs and
the replacement of one species by another. In Norway Brun (1972) reported
that Northern Gannets have ousted Common Murres (=Guillemots) and Black-leg-
ged Kittiwakes from breeding sites in two of four colonies. Similarly, in
New Zealand, Cape Gannets have taken over the traditional breeding sites of
White-fronted Terns (Reed, 1979). On Skomer Island Manx Shearwaters exclude
Atlantic Puffins from burrows they would otherwise use, particularly affect-
ing young adult puffins unable to successfully compete for burrows (Harris,
1966). Belopol'skii(1957) also reported competition for nest sites among spe-
cies: Thick-billed Murres sometimes take over Kittiwake nests; and Common

Murres take over nests of Thick-billed Murres, Auks and Puffins, and the
cliff-top nests of eiders, geese and Black Guillemot. Cassin's Auklets and
Rhinoceros Auklet similarly compete for nest sites, and the density of Rhi-
noceros Auklet burrows affects the presence of Cassin's Auklets (Vermeer,
1979). Under some circumstances, kittiwakes can replace nesting Fulmars
(Coulson, Horobin, 1972). In larid colonies, the larger species often takes
over nest sites of smaller species, eventually eliminating them from these
colonies (Vermeer, 1970; Morris, Hunter, 1976; Furness, 1977; Burger, Shis-
ler, 1979). Larger larids often arrive at the colony sites earlier than smal-
ler species, suggesting temporal factors may play a role.

Clearly size and arrival times are important factors determining the win-
ner of interspecific competition for nest sites. However, smaller species
that arrive later can acquire nest sites if they intrude as a dense group
rather than as individuals. For example, Blue-faced Boobies can win against
larger Laysan Albatross on Kure Atoll (Kepler, 1969), dense-nesting Arctic
Terns can evict Herring Gulls (Bianki, 1977), and Sandwich Terns arriving
later than Black-headed Gulls succeed in moving into the center of the colo-
ny, displacing the two or three resident territory holders (Taverner, 1969).

For some species, there are added benefits of mixed species colonies:
petrels use burrows excavated by Tufted Puffins (Boersma et al., 1980), Cas-
sins' Auklets (Thoreson, 1964), and Atlantic Puffins (Cramps et al., 1974);
and Fulmars occupy the sites of Shags after the latter have bred. In summary,
interspecific competition for nest sites exists in some colonies, but not at
others. Assuming complete displacement does not occur, a species will usually

have more competition from conspecifics that require similar sites than from heterospecifics with different requirements.

Nest Materials: Competition for nest materials is a disadvantage of nesting in both monospecific and mixed-species colonies. Presumably interspecific competition will be intense when requirements for materials are similar (i.e. frigatebirds, Diamond, 1975a), but will be less where requirements differ. Thus, given the same number of pairs in a colony, the presence of heterospecifics should lessen competition for nest materials.

Mates: Since competition for mates is restricted to conspecifics, mixed-species colonies of equal numbers of nesting birds as monospecific colonies will have lower levels of mate competition than monospecific colonies.

Food: Competition for food is a potential disadvantage of nesting in colonies since members do not obtain food from their individual territories but gather food in the area around the colony. The area around each colony where birds obtain their food depends on the foraging behaviour of each species, food availability, and amount of suitable foraging habitat. One advantage often attributed to colonial nesting is the increased potential for exploitation of patchily-distributed food resources (Ward, Zahavi, 1973). Presumably, members of a colony obtain information about food sources from colony mates, whereas a solitary nester might be unable to locate food patches. For heterospecifics information transfer and local enhancement would function only if two or more species use the same foods and can obtain information about food sources from heterospecifics.

Interspecific competition for food has been examined for a number of species, and differences in foods consumed have been shown for most species. Volkman et al. (1980) found differences in size of prey items taken (Euphausia spp.) by three species of penguins breeding in Antarctica, although krill made up most of the diet of all three. Similarly, Berruti (1979) showed that Sooty and Light Mantled Albatross ate different foods; Diamond (1975a) reported that Great and Lesser Frigatebirds are similar prey items although the latter preferred squid over fish; Nelson (1975) found that frigatebirds caught prey by surface dipping and aerial snatching, and did not exploit food in deeper ocean layers available to boobies, tropic birds, cormorants and pelicans ; Diamond (1975b) reported that on Aldabra Atoll Red-tailed Tropic birds take larger fish and feed farther from land than White-tailed Tropic bird, and Vermeer (1979) showed that Rhinoceros Auklets feed at night while Tufted Puffins feed on different fish during the day. Blus, Prouty, Neely (1979) showed that while nesting in the same colony 63% of the diet of Sandwich Terns was shrimp and anchovies whereas 57% of the diet of Royal Terns was Menhaden (Brevoortia tyrannus). Similarly, Lemmetyinen (1976) showed difference in feeding habitat and foods taken between Arctic and Common Terns in Finland. Witt et al. (1981) showed that Audouin's and Herring Gulls breeding on Mediterranean Islands used different foods; Audouin's Gull fed on fish (over 90%) obtained coastally by fishing while Herring Gulls fed mainly on plant material, birds, and fish obtained from human sources. Unlike most studies, Belopol'skii (1957) compared the diets of several taxonomically diverse seabirds in the Barents Sea (Table 3) and found that fish comprised 0-97% of the diet of these species, with alcids taking the highest percentage of fish.

Table 3. Food Competition among seabirds at East Murman, Russia (after Belopolskii, 1957) x = > 70% diet, y = > 70%, () = %

| | Fish | Crustaceans | Molluscs | Insects | Birds & Mammals | Berries |
|---|---|---|---|---|---|---|
| Common Eider | (0) | Y | x | | | |
| Arctic Skua | x (62) | | Y | Y | Y | Y |
| Herring Gull | x (53) | Y | Y | Y | Y | Y |
| Black-backed Gull | x (73) | | Y | Y | Y | Y |
| Mew Gull | y (39) | Y | Y | Y | | Y |
| Arctic Tern | x (55) | Y | | Y | | |
| Black-legged Kittiwake | x (71) | Y | Y | Y | | |
| Black Guillemot | x (73) | Y | | | | |
| Puffin | x (87) | Y | | | | |
| Thick-billed Murre | x (90) | Y | | | | |
| Common Murre | x (96) | | | | | |
| Razor-billed Auk | x (97) | | | | | |

These examples indicate interspecific overlap in food items, with a reduction in competition through differences in size and type of prey, habitat selection, foraging techniques, and time of foraging. No study has shown 100% overlap in even one of these parameters (with the possible exception of the Antarctic Penguins). Nonetheless, the overlap is less than among conspecifics. Given the same number of individuals in a colony, competition for food should be less in mixed-species colonies compared to monospecific colonies: particularly when colonies are comprised of birds from different taxonomic families. However, overlap in foods used does not prove competition, which requires limited resources. Some authors have suggested that when food is scarce it is unavailable to all birds causing general starvation, not selective starvation of those less able to "compete" (Vermeer et al., 1979).

Overlap in foods makes it possible for information transfer to occur. Proofs of information transfer are difficult to obtain even in monospecific colonies, partly because this mechanism would not have to operate at all times to be selected for. Krebs (1974) tested the hypotheses of information transfer in Great Blue Herons (Ardea herodias) and reported that birds departed from the colony non-randomly, birds from neighboring nests left together, and flock feeders had higher success than solitary feeders. In seabirds, synchrony of departure from colonies has been found for murres and puffins (Ashcroft, 1979) although no one has examined synchronous departure of heterospecifics from seabird colonies.

Mixed species foraging flocks are very common (Sealy, 1973). Hoffman et al. (1982) found that some species act as catalysts in mixed species flocks, suggesting an advantage to non-catalysts of nesting in colonies with catalysts (larids and shearwaters). Away from colonies, birds may be attracted to evidence of a food source such as diving terns (local enhancement, Gochfeld,

Burger, 1981). Caldwell (1981) examined mixed-species heron flocks, and found that herons were attracted to the presence of models, indicating that local enhancement occurs. However, such experiments do not test for information transfer within colonies. Theoretically the potential for information transfer is less in mixed species colonies compared to monospecific colonies because each species uses different prey items and foraging techniques. Although Bayer (1982) argued that information transfer could not have been a factor in the evolution of coloniality since a colony must already exist for it to occur, I submit that mixed species colonies could have information transfer as a selective factor. Birds already using information on food sources from conspecifics could easily begin to use information from heterospecifics.

## Predation and Predator Protection

Birds are exposed to predators whether they nest solitarily or in monospecific or mixed-species colonies. However, many predators and pirates nest within mixed-species colonies. In this section I discuss predators and pirates nesting within mixed-species colonies; and anti-predator behavior of colony members.

Predators: Two types of predators nest in mixed species colonies, colonial birds that normally associate with particular species, and those that sometimes nest in mixed species colonies but usually nest solitarily. The large, white-headed gulls are predators that nest with many other seabirds (refer to Table 2). Herring, Great Black-backed, Glaucous, Western, Dolphin, Kelp and California gulls prey on the eggs and young of colony members including Jackass Penguins (Rowlands, 1981), Gannets (Taylor, Wodzicki, 1958), White Pelicans (Schaller, 1964), Storm Petrels, Manx Shearwater and Atlantic Puffins (Harris, 1980; Nettleship, 1972), Double-crested Cormorants and King Shags (Kury, Gochfeld, 1975), Cassin's Auklet (Thoresen, 1964) and Thick-billed Murres (Birkhead, Nettleship, 1981). The large gulls frequently eat the eggs of similarly-sized congenerics (Brown, 1967) and eggs of smaller larids such as Black-headed Gulls (Kruuk, 1964), Laughing Gulls (Burger, 1979), Ring-billed Gulls (Vermeer, 1970), Common and Arctic Terns (Lemmetyinen, 1971). Small gulls such as Laughing Gulls will occasionally prey on the eggs of terns (Blus et al., 1979; Burger, Lesser, 1978). Predation by gulls on smaller species often leads to desertion of colony sites by smaller species (Morris, Hunter, 1976; Burger, 1979). Indeed Black Skimmers are more likely to desert colony sites after failure due to predation than to flooding (Burger, 1982). Gulls inflict considerable damage: Harris (1980) reported that 40 pairs of Great Black-backed Gulls nesting in a Puffin colony killed 1.5% of the adult breeding population annually (2600 Puffins/year). Predation rates were highest in low density-nesting areas. Gulls cause Puffins to leave their burrows by giving alarm calls; at each disturbance departing Puffins displace 13-17% of their eggs to burrow entrances where gulls eat them (Nettleship, 1972).

Two other seabirds are predators on colony mates: skuas and frigatebirds. Frigatebirds take the eggs and young of other seabirds (Nelson, 1975) and congenerics (Nelson, 1968; Schreiber, Ashmole, 1970). But since frigatebirds usually nest in monospecific colonies, their effect on other species is di-

minished. Skuas, however, are formidable predators in any colony where they nest. The effect of Antarctic Skuas on penguins and petrels (Tenaza, 1971; Young, 1978) congenerics, and other seabirds (Furness, 1981) is great. The relationship between Adelie Penguins and South Polar Skuas is complex: skuas keep other skuas out of their territory, and penguins nesting within this territory are exposed to predation only from resident skuas that usually eat deserted eggs and chicks, and are unable to acquire incubated eggs, or chicks in creches (Young, 1978). Predation is greater on edge-nesting penguins unprotected by territorial skuas, where two or more skuas cooperate to distract parent. In eight breeding seasons, Great Skuas ate eggs and young of conspecifics, Puffin, Kittiwake, Parasitic Jaeger, Fulmar, Storm Petrel, shag, gulls, Black Guillemot and Arctic Tern with jaegers sustaining the highest population loss (22%) each year (Furness, 1981).

Non-seabird predators also nest in seabird colonies (crows, night-herons). Crows nesting adjacent to Pelagic and Double-crested Cormorant colonies in British Columbia ate cormorant eggs (Verbeek, 1982). Black-crowned Night Herons (<u>Nycticorax nycticorax</u>) ate eggs and chicks of Common Terns at an Ontario colony, causing temporary desertion of adults and lowered reproductive success (Hunter, Morris, 1976). At Agassiz National Wildlife Refuge I found Black-crowned Night Herons nesting in Franklin's Gull colonies, shifting locations with the gulls. The gulls did not eat eggs of gulls or night-herons, but the night-herons ate the eggs and young in most gull nests within 10 m of their nests.

Pirates: Stealing food from conspecifics or other species occurs where birds are foraging, or feeding young at colonies. Some pirates nest in mixed species colonies. On Marion Island, Lesser Sheathbills (<u>Chionis minor</u>) stole most of their food from penguins feeding their chicks crustaceans, fish and squid (Burger, 1979). Red-tailed Tropic birds on Kure Atoll are often forced to disgorge their food to Great Frigatebirds (Woodward, 1972). Larids are the most frequent pirates that nest in seabird colonies: Laughing Gulls rob food from Sandwich and Royal terns (Blus et al., 1979), Herring and Great Black-backed Gulls pirate from Puffins (Nettleship, 1972), and Silver Gulls rob Lesser Crested and Crested Terns (Hulsman, 1976). Such piracy can reduce reproductive success: Nettleship (1972) reported that where gulls nested 37% of Puffin nests fledged young compared to 90% on Funk Island where gulls did not nest with Puffins.

Antipredator Behaviour: Birds nesting in colonies have several methods of protection from predators including early warning, predator defense and passive "predator swamping". These advantages work less well in colonies where predators nest, since birds habituate to them. But, where predators nest outside the colony, interspecific warning can occur, each species can give early warning, and the species giving the first warning may vary. I have observed this in mixed species colonies of Herring and Great Black-backed Gull; Herring and Laughing Gulls; Laughing Gull and Common Tern; and in mixed species colonies of ardeids. Further, recognition of warning signals cuts across familial lines as Black Guillemots in burrows respond to the warning cries of shorebirds, and larids (Bianki, 1977), and puffins, herons, terns, and cormorants respond to gull calls (Nettleship, 1972; Burger, unpub. data). For burrowing

species, the advantage of above-ground heterospecifics giving warning calls is obvious.

Direct defense behaviors such as chasing or mobbing predators are effective for several species (see: Kruuk, 1964; Burger, 1981) and should be effective whether the mobbing is performed by one or several species. Mobbing does involve a cost, as predators sometimes take a diving bird (Myers, 1978). For most species in mixed species colonies, the effect of mobbing is equal regardless of who mobs. However, some species do not mob, and derive advantages from heterospecifics that do. Sandwich Terns depend upon the pugnaceousness of nearby Black-headed Gulls to chase predators away, and shift colony sites along with them (Nehls, 1969; Smith, 1975). Although gulls try to eat tern eggs, the terns can defend them (Lind, 1963). Other examples of protective associations include: Caspian Terns with other larids (Bergman, 1980), Gull billed Terns with Black-headed Gulls (Moller, 1981), Common Gulls with Parasitic Jaeger (Gotmark, Andersson, 1980), and Black Skimmers with Common Terns (Burger, Lesser, 1978). Protective associations are not restricted to seabirds (see Nuechterlein, 1981).

One anti-predator strategy given as a cause of birds nesting in colonies is increased social facilitation which increases breeding synchrony, results in young produced over a short period of time, and effectively "swamps predators" (Darling, 1938; Burger, 1979; Gochfeld, 1980). Presumably some social facilitation occurs among species in mixed species colonies (Orians, 1961). Hilden (1965) noted that Little Gulls need the facilitation of colonies of terns and Black-headed gulls to become established, and Bergman (1980) indicated the importance of other larids to Caspian Terns establishing themselves in the Baltic. The social stimulation of cormorants is essential to the establishment of Gannet colonies in Norway (Brun, 1972). I have observed lone pairs of Black Skimmers nesting in Common Tern colonies, while solitary pairs of nesting skimmers do not occur. Obviously these birds obtained some "social benefit" from heterospecifics.

Disease and Parasites: Birds in colonies are exposed to increased loads of parasites and diseases because they are in close proximity and interact daily. Many parasites are able to use more than one seabird species as a host (Hindwood et al., 1963) suggesting that mixed species colonies do not completely reduce the risk of parasitism. This aspect of seabird biology needs further study.

SUMMARY

The advantages and disadvantages of mixed species colonies relate to resource allocation, predation and disease. Birds in mixed species colonies compete for nest sites, materials and food, and must avoid predation and disease. Colonies are obvious to predators, but they can be in inacessible sites. Colony defenses include mobbing and early warning. Social facilitation is a mechanism to increase breeding synchrony which lowers predation through "predator swamping"; and information transfer is a mechanism to obtain information about nesting sites, impending danger, and food. These advantages operate in monospecific colonies, but the disadvantages of competition for food, nest materials and nest sites are lessened in mixed-species colonies since heterospecifics do not have exactly the same requirements. For

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many species, mixed species colonies may be a result of habitat pressure. Heterospecifics increase the effective colony size for predator detection, predator protection, social facilitation and information transfer, while lessening competition for space. Some species derive most of their predator protection from mixed-species associations, seeking out protector species. Thus, nesting in mixed-species colonies reduces the costs of competition and allows the benefits of social faciliation and predator protection to remain constant or increase in protective associations.

ACKNOWLEDGMENTS

APPENDIX **A**. Advantages and Disadvantages of Mixed-Species Colonies of Seabirds

I    Advantages
  A. Predator Protection
    1. Early warning
    2. Predator defense
      a. mob predator
      b. attack predator
    3. "Predator Swamping"
  B. Resource Utilization
    1. Food
      a. Decreased competition for food compared to equal number of conspecifics
      b. Information transfer and local enchancement of food sources
      c. Direct source of food for kleptoparasites or predators nesting within colonies
    2. Nest sites
      a. Different species-slightly different requirements
      b. Burrows excavated by one species can be used by another
    3. Nest materials
  C. Colony Establishment
    1. Indication of safe nesting sites
    2. Nucleus for solitary or small number of colonizers
II   Disadvantages
  A. Predator and Kleptoparasite Enchancement
    1. Colonies are easier to detect with diversity of cues from different species
    2. Predators and Kleptoparasites often nest within colonies, and are attracted to colonies
    3. Different species might result in longer total breeding period (reduce the effect of "predator swamping")
  B. Competition
    1. Nest sites and materials
    2. Food
  C. Disease Transmission
  D. Interspecific Aggression

914

APPENDIX B: Seabird Species Mentioned in Text

Gentoo Penguin (Pygoscelis papua)
Adelie Penguin (Pygoscelis adeliae)
Chinstrap Penguin (Pygoscelis antarctica)
Erect-crested Penguin (Eudyptes sciateri)
Rockhopper Penguin (Eudyptes crestatus)
Jackass Penguin (Spheniscus demersus)
Black-footed Albatross (Diomedea nigripes)
Laysan Albatross (Diomedea immutabilis)
Sooty Albatross (Phoebetria fusca)
Light-mantled Albatross (Phoebetria palpebrata)
Fulmar (Fulmarus glacialis)
Wedge-tailed Shearwater (Puffinus pacificus)
Christmas Shearwater (Puffinus nativitatus)
Manx Shearwater (Puffinus puffinus)
Storm Petrel (Hydrobates pelagicus)
Madeiran Storm Petrel (Oceanodroma castro)
Red-billed Tropic bird (Phaethon aethereus)
Red-tailed Tropic bird (Phaethon rubricauda)
White-tailed Tropic bird (Phaethon lepturus)
White Pelican (Pelecanus erythrorhynchos)
Northern Gannet (Sula bassana)
Cape Gannet (Sula capensis)
Blue-faced Booby (Sula dactylatra)
Brown Booby (Sula leucogaster)
Red-footed Booby (Sula sula)
Double-crested Cormorant (Phalacrocorax auritus)
Shag (Phalacrocorax aristotelis)
Pelagic Cormorant (Phalacrocorax pelagicus)
King Cormorant (Phalacrocorax albiventer)
Great Frigatebird (Fregata minor)
Lesser Frigatebird (Fregata ariel)
Great Skua (Catharacta skua)
South Polar Skua (Catharacta maccormicki)
Antarctic Skua (Catharacta antarcticus)
Parasitic Jaeger (Stercorarius parasiticus)
Audouin's Gull (Larus audouinii)

Ring-billed Gull (Larus delawarensis)
Herring Gull (Larus argentatus)
Lesser Black-backed Gull (Larus fuscus)
California Gull (Larus californicus)
Western Gull (Larus occidentalis)
Kelp Gull (Larus dominicanus)
Great Black-backed Gull (Larus marinus)
Glaucous Gull (Larus hyperboreus)
Laughing Gull (Larus atricilla)
Franklin's Gull (Larus pipixcan)
Silver Gull (Larus novaehollandiae)
Black-headed Gull (Larus ridibundus)
Slender-billed Gull (Larus genei)
Little Gull (Larus minutus)
Black-legged Kittiwake (Rissa tridactyla)
Caspian Tern (Sterna caspia)
Common Tern (Sterna hirundo)
Arctic Tern (Sterna paradisaea)
Gray-backed Tern (Sterna lunata)
White-fronted Tern (Sterna striata)
Crested Tern (Sterna bergii)
Lesser Crested Tern (Sterna bengalensis)
Royal Tern (Sterna maxima)
Sandwich Tern (Sterna sandvicensis)
Brown Noddy (Anous stolidus)
Black Noddy (Anous tenuirostris)
Black Skimmer (Rynchops niger)
Razorbill Auk (Alca torda)
Thick-billed Murre (Uria lomvia)
Common Murre (Uria aalge)
Black Guillemot (Cepphus grylle)
Pigeon Guillemot (Cepphus columba)
Rhinoceros Auklet (Cerorhinoa monocerata)
Atlantic Puffin (Fratercula arctica)
Tufted Puffin (Lunda cirrhata)

R e f e r e n c e s

Amerson A.B. Jr., Clapp R.B., Wirtz W.O. - Atoll Research Bull., 1974, 11, p. 174-306.

Amerson A.B. Jr., Shelton P.C. - Atoll Research Bull., 1976, 192, p. 1-479.

Anderson D.W., Bartonek J.C. - Condor, 1967, 69, p. 311-313.

Ashcroft R.E. - Ornis, Scand., 1979, 10, p. 100-110.

Bayer R.D. - Auk, 1981, 99, p. 31-40.

Belepol'skii L.O. - Ecology of Sea Colony Birds of the Baerents Sea. Moscow, 1957.

Beck J.R., Brown D.W. - Ibis, 1971, 113, p. 75-90.

Bedard J. - Condor, 1969, 71, p. 386-398.

Bergman G. - Ornis Fennica, 1980, 57, p. 141-152.

Berruti A. - Emu, 1979, 79, p. 161-175.

Bianki V.V. - Bulls, shorebirds and alcids on Kandalaksha Bay. Israel,1967.

Birkhead T.R., Nettleship D.N. - Auk, 1981, 98, p. 258-269.

Blus L.J., Prouty R.M., Neely B.S. Jr. - Biol. Cons., 1979, 15, p. 301-320.

Boersma P.D., Wheelwright N.T., Nerini M.K., Wheelright E.S. - Auk, 1980, 97, p. 268-282.

Brown R.G.B. - Ibis, 1967, 109, p. 502-515.

Brun E. - Astarte, 1971, 4, p. 53-60.

Brun E. - Ornis, 1972, Scand., 3, p. 27-38.

Burger A.E. - Ardea, 1979, 67, p. 1-14.

Burger J. - Condor, 1979, 81, p. 269-277.

Burger J. - Quart. Rev. Biol., 1981, 56, p. 143-167.

Burger J. - Auk, 1982, 99, p. 109-115.

Burger J., Lesser F. - Ibis, 1978, 120, p.433-449.

Burger J., Shisler J. - Auk, 1978, 95, p. 252-265.

Burger J., Miller L.M., Hahn D.C. - Wilson Bull., 1978, 90, p. 359-375.

Caldwell G.S. - Behav. Ecol. Sociobiol., 1981, 8, p. 99-103.

Clapp R.B., Kridler E. - Atoll Research Bull., 1977, 20, p. 1-102.

Clapp R.B., Wirtz W.O. - Atoll Research Bull., 1975, 186, p. 1-196.

Coulson J.C., Horobin J.M. - Ibis, 1972, 114, p. 30-42.

Cramp S., Bourne W.R.P., Saunders D. - Seabirds of Britain and Ireland. New York, Taplinger Publ. Co.

Darling F.F. - Bird Flocks and the Breeding Cycle. London, Cambridge U. Press, 1938.

Diamond A.W. - Condor, 1973, 75, p. 200-209.

Diamond A.W. - Ibis, 1975a, 117, p. 302-323.

Diamond A.W. - Auk, 1975b, 92, p. 16-39.

Drent R.H., Guiguet C.J. - Occ. Paper British Columbia Mus, 1961, 12, p. 1-173.

Ellison L.N., Cleary L. - Auk, 1978, 95, p. 510-517.

Erwin R.M. - Ani. Behav., 1979, 27, p. 1054-1062.

Evans P.G.H. - Ibis, 1981, 123, p. 1-18.

Furness R.- Brit. Birds, 1977, 70, p. 96-107.

Furness R. - Seabird Report, 1981, 6, p. 5-12.

Furness R.W., Baillie S.R. - Ringing and Migration, 1981, 3, p. 137-148.

Frings H., Frings M. - Condor, 1961, 63, p. 304-312.

Gallagher M.D. - Ibis, 1960, 102, p. 489-506.

Gochfeld M. - In: Behavior of Marine Animals IV. Marine Birds / Eds. J.Burger, B.Olla, H.Winn. New York,Plenum Press, 1980, p. 207-270.

Gochfeld M., Burger J. - Behav. Ecol., Sociobiology, 1981, 10, p. 15-17.

Gotmark F., Andersson M. - Ornis, Scand., 1980, 11, p. 121-126.

Grant P.R., Nettleship D.N. - Ornis, Scand., 1971, 2, p. 81-87.

Harris M.P. - Nature in Wales, 1963, 8, p. 56-58.

Harris M.P. - Ibis, 1966, 108, p. 17-33.

Harris M.P. - Ibis, 1969, 111, p. 139-156.

Harris M.P. - Ibis, 1973, 115, p. 483-510.

Harris M.P. - Condor, 1974, 76, p. 249-261.

Harris M.P. - Ibis, 1980, 122, p. 193-209.

Harris M.P., Bode K.G. - Emu, 1981, 81, p. 20-28.

Hilden O. - Ann. Zool. Fennici, 1965, 2, p. 53-75.

Hindwood K.A., Keith K., Servently D.L. - Div. Wildlife Technical Paper, 1963, 3, p. 1-44.

Hoffman W., Heinemann D., Wiens J.A. - Auk, 1981, 98, p. 437-456.

Hulsman K. - Emu, 1976, 76, p. 143-149.

Hunt G.L. Jr., Pitman R.L., Jones H.L. - In: The Californial Islands / Ed. by D.M.Powers, 1980, p. 443-459.

Hunter R.A., Morris R.D. - Auk, 1976, 93, p. 629-633.

Jouventin P., Guillotin M. - Rev. Ecol., 1979, 33, p. 109-127.

Kepler C.B. - Auk, 1967, 84, p. 426-430.

Kepler C.B. - Pub. Nuttall Ornithological Club, 1969, 8, p. 1-97.

Kepler C.B., Kepler A.K. - Living Bird, 1977, 16, p. 21-50.

Krebs J.R. - Behaviour, 1974, 51, p. 99-134.

Krunk H. - Behaviour Suppl., 1964, 11, p. 1-129.

Kury C.R., Gochfeld M. - Biol. Cons., 1975, 8, p. 23-34.

Lemmetyinen R. - Ornis Fenn., 1971, 48, p. 13-24.

Lemmetyinen R. - Auk, 1976, 93, p. 636-640.

Lid G. - Fauna Norv. Ser. C, 1980, 4, p. 30-39.

Lind H. - Dansk Ornith. Foren. Tidsskrift, 1963, 57, p. 155-175.

Manuwal D.A., Manuwal N.J. - Western Birds, 19, p. 189-200.

Moller A.P. - Ardea, 1981, 69, p. 193-198.

Morris R.D., Hunter R.A. - Canadian Field Naturalist, 1976, 90, p. 137-143.

Morrison M.L., Shanley E. Jr., Slack R.D. - Southwest Naturalist, 1979, 24, p. 259-266.

Morse D.H., Buchheister C.W.- Bird-band., 1977, 48, p. 340-349.

Murbarger N. - Natural History, 1956, p. 298-305.

Myers P. - Auk, 1978, 95, p. 419-420.

Nehls H.W. - Vogelwarte, 1969, 25, p. 52-57.

Nelson J.B. - Nature (L.), 1967, 214, p. 318.

Nelson J.B. - Galapagos, Islands of Birds. L.: Longmans, 1968.

Nelson J.B. - Living Bird, 1975, 14, p. 113-156.

Nettleship D.N. - Ecol. Monogr., 1972, 42, p. 239-268.

Nuechterlein G.S. - Anim. Behav., 1981, 25, p. 985-989.

Orians G.H. - Condor, 1961, 63, p. 330-337.

Prince P.A. - Ibis, 1980, 122, p. 476-488.

Prys-Jones R.P., Peet C. - Ibis, 1980, 122, p. 76-81.

Reed S. - Nortornis, 1979, 26, p. 89-93.

Richardson F. - Condor, 1961, 63, p. 456-473.

Richdale L.E. - Ibis, 1964, 106, p. 110-114.

Roby D.D., Brink K.L., Nettleship D.N. - Arctic, 1981, 34, p. 241-248.

Rowlands B.W. - Bokmokierie, 1981, 33, p. 21-24.

Schaller G.B. - Condor, 1964, 66, p. 3-23.

Schrieber R.W., Ashmole N.P. - Ibis, 1970, 112, p. 363-394.

Sealy S.G. - Auk, 1973, 90, p. 796-802.

Smith A.J.M. - Brit. Birds, 1975, 68, p. 142-156.

Spellerberg I.F.- Ardea, 1971, 59, p. 189-229.

Stone W. - Bird Studies at Old Cape May. New York, Dover, 1937.

Stonehouse B. - Ibis, 1962, 103b, p. 409-422.

Taverner J.H. - Seabird Report, 1969, p. 46-47.

Taylor R.H., Wodzicki. - Notornis, 1958, 8, p. 22-23.

Tenaza R. - Condor, 1971, 78, p. 81-92.

Thoresen A.C. - Condor, 1964, 66, p. 456-476.

Tickell W.L.N., Pinder P. - Ibis, 1975, 117, p. 433-451.

VanGessel F.W.C. - Corella, 1978, 2, p. 52-53.

Verbeek N.A.M. - Auk, 1982, 99, p. 347-352.

Vermeer K. - Canadian Wildlife Report, 1970, N 12, p. 1-52.

Vermeer K. - Ardea, 1979, 67, p. 101-110.

Vermeer K., Cullen L. - Ardea, 1979, 67, p. 22-27.

Vermeer K., Vermeer R.A., Summers K.R., Billings R.R. - Auk, 1979, 96, p.143-151.

Verner J. - Auk, 1961, 78, p. 573-594.

Volkman N.J., Presler P., Trivelpiece W. - Condor, 1980, 82, p. 373-378.

Ward P., Zahavi A. - Ibis, 1973, 115, p. 517-534.

Warham J. - Auk, 1963, 80, p. 229-256.

Warham J. - Ardea, 1972, 60, p. 145-183.

Warham J., Keeley B.R., Wilson G.J. - Auk, 1977, 94, p. 1-17.

White M.G., Conroy J.W.H. - Ibis, 1975, 117, p. 371-373.

Williams A.J. - Ornis, Scand., 1974, 5, p. 113-121.

Witt H.H., Cresppo J., Suana E.D., Varela J. - Ibis, 1981, 123, p. 519-526.

Wood R.C. - Auk, 1971, 88, p. 805-814.

Woods R.W. - Ibis, 1970, 112, p. 15-24.

Woodward P.W. - Atoll Research Bull., 1972, 164, p. 1-318.

Young E.C. - Ibis, 1963, 105, p. 203-233.

Young E.C. - New Zealand Jour. Zoology, 1978, 5, p. 401-416.

# SOME FURTHER COMMENTS ON THE GATHERINGS OF BIRDS

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I have been asked by Dr. Burger to use the available time, owing to the absence of Dr. Nettleship to add some comments on the function of the gatherings of birds as information centers (Ward, Zahavi, 1973). Some of these comments are the outcome of discussions with the late Dr. P. Ward whose recent tragic death ended for me a very fruitful collaboration. Consider these comments as comments to a discussion rather than as a paper in the symposium.

1. Since we have published the hypothesis there have been a few attempts to gather evidence to test the hypothesis. A few attempts have failed to secure evidence for the hypothesis (Evans, 1982; Bayer, 1982). When looking for such evidence it is important to remember that although information concerning the location of food may sometimes be of use, birds are not necessarily in search of such information every day. In order to secure supporting evidence it may be necessary to watch at particular days following a sudden decline of food. I shall cite an observation by Dr. Pearse (pers.comm.) to illustrate the case. Rooks (Corvus frugilegus) around Aberdeen breed in Colonies in which trey also roost in summer. But in winter several colonies gather for the night roost. In the morning the rooks fly first to their respective colonies and later always forage within the homerange of the colony. Further there is evidence that food is more abundant in winter than it is in summer. These findings seem to contradict the hypothesis that the communal roost serves for rooks as an information center. But once, during a snow storm when most of the ground was covered with snow and visibility was very low, a whole colony followed another colony, from the night roost, to feed together on a stack of corn available above the snow. It is reasonable to believe that unless the rooks at that time had information about food they would not have been able to survive. It may be that such rare cases are sufficient to select for the communal roost.

2. Birds are attracted to the communal roost by the communal displays which occur in most communal roosts sometime before the birds go into the roost. In 1973 we suggested that the displays function as "advertisement to facilitate the assembly into a single roost of as many birds as possible, from as far away as possible. The more birds attending a particular roost, the larger is the area searched for food and the greater is the chance of all good feeding places within it being decovered". Although the displays serve to advertise it is a mistake to consider the advertisement as an ultimate reason (as we did) for the behaviour of the individual bird in the flock. Stated as it is, it is a group selection argument. A bird may rest in the periphery of the roost and enjoy the outcome of the advertisement without investing in it. Those who are not satisfied in explanations by models of group selection should consider an alternative explanation.

I suggest that a bird which displays with others is able to assess its potential to compete with its flock members when they would eventually reach the feeding site. There is often no point to arrive at a feeding site if all

other members of the flock are quicker and stronger. Such a hypothesis suggest that the strength, agility and other performances of individuals in various flocks differ to the extent that a bird may benefit from picking the flock which suits its potential. Such a hypothesis may be tested.

3. Birds watching daily the gatherings into a communal roost may acquire some information on the homerange of their roost without having to go out of their individual homerange. If the numbers of birds in the roost increases they would benefit if they stay because if it is good for the new arrivals the home range of the roost may still serve them if they loose their feeding sites, on the otherhand if numbers decline in the roost they may also do well if they leave before they are actually short of food.

4. I still believe that a gathering without active defence is not an effective strategy to reduce predation pressure in birds. Although predation certainly affect much of the behaviour of the birds in the gathering, predation pressure by itself has not selected birds to gather into roosts or nesting colonies.

5. In 1973 we have overlooked the importance of sexual selection as a primary factor in selecting birds to form leks and nesting colonies. There is now some evidence to show that leks may function as advertisement for the fitness of the males. Males in the center of a lek have a much higher fitness than peripheral males. Thus leks function for females as information centers to leatn about the fitness of their potential mates and for males to advertise their fitness. Coulson (this symposium) has provided evidence to show that in Kittiwakes, Rissa tridactyla, the nesting colony may function as advertisement to the fitness of the males and that females prefer central males to peripheral males.

**PHYSIOLOGY OF REPRODUCTION, MOULT AND MIGRATION**

Convener: D.S. FARNER, USA
Co-conveners: I. ASSENMACHER, FRANCE; P. BERTHOLD, FRG


BERTHOLD P.

ENDOGENOUS COMPONENTS OF ANNUAL CYCLES OF MIGRATION AND MOLT


NOSKOV G.A., RYMKEVICH T.A.

PHOTOPERIODIC CONTROL OF POSTJUVENILE AND POSTNUPTIAL MOLTS IN **PASSERIFORMES**


JALLAGEAS M., ASSENMACHER I.

ENDOCRINE CORRELATES OF MOLT AND REPRODUCTIVE FUNCTION IN BIRDS


MOORE M.C., FARNER D.S., DONHAM R.S., MATT K.S.

ENDOCRINE AND PHOTOPERIODIC RELATIONSHIPS DURING PHOTOREFRACTO-RINESS, POSTNUPTIAL MOLT, AND ONSET OF MIGRATION IN **ZONORITCHIA LEUCOPHRYS GAMBELII**


NOVIKOV B.G., RUDNEVA L.M., BULDAKOVA A.N., IVANOVA L.S., GARMATI-NA S.M.

THE ROLE OF THE HYPOTHALAMO–HYPOPHYSIAL SYSTEM IN THE ANNUAL CYCLE OF MOLT AND GONADAL FUNCTION

# ENDOGENOUS COMPONENTS OF ANNUAL CYCLES OF MIGRATION AND MOULT

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## INTRODUCTION

During the past two decades a steadily increasing body of evidence indi‑
cates that endogenous components are involved in the control of annual proces‑
ses in birds. Among European-African long-distance migrants in which such
components have been extensively demonstrated it seems that annual periodi‑
city is based on endogenous components. The most important endogenous func‑
tions of these species are the so-called circannual rhythms. As shown at the
last International Ornithological Congress (Berthold, 1980), they have been
proven to be true biological clocks, i.e. self-sustained internal rhythms,
at least in part with life-long efficacy. In addition, circannual rhythms
have been shown to control at least seven different annual processes in birds
including migration and moult (e.g., Gwinner, 1981).

More recently, convincing evidence has been accumulated that these inter‑
nal rhythms can reflect species- and population-specific temporal programs
and thus are important for the detailed time course of individual annual pro‑
cesses. In some cases these control mechanisms have been demonstrated to
have a genetic basis. The following sections will concentrate on innate en‑
dogenous components involved in migratory activity and moult, in the control
of some morphological features associated with migration, and on the innat‑
eness of the migratory urge.

## ENDOGENOUS PATTERNS OF MIGRATORY DISPOSITION AND RESTLESSNESS: INSENSITIVITY TO EXTERNAL INFLUENCES

Over the past nine years we have carried out a set of eight experiments
under defined conditions on the garden warbler, Sylvia borin, to test en‑
vironmental influences on the changes of body weight and migratory restless‑
ness seen during the migratory period. The results are depicted schematical‑
ly in Fig. 1. The upper graphs show the time course of body weight during the
migratory period, the lower those of nocturnal restlessness. Solid lines re‑
present data from control groups, broken ones those from experimental groups.
All data were obtained from groups of at least the hand-raised individuals
during their first autumnal migratory period.

Part A shows the normal pattern of body weight and restlessness during
the migratory period from about July to the end of the year as they are ex‑
pressed in natural light conditions as well as in various constant experi‑
mental conditions. B refers to an experiment, in which Gwinner (1974) almost
completely depressed restlessness by darkening during the night for a period
of two months. Despite this treatment, the subsequent course of restlessness
in the experimental group was parallel to that of the control group and
proved to be uninfluenced by the previous treatment. In two other experi‑

F i g. 1. Schematic presentation of the normal course (A) of changes in body mass (above) and of migratory restlessness (below) in Sylvia borin, and data from seven experiments (B–H) to test the effects of environmental influences on these patterns. Broken lines: data from experimental groups, solid lines: data from control groups. For details, see text
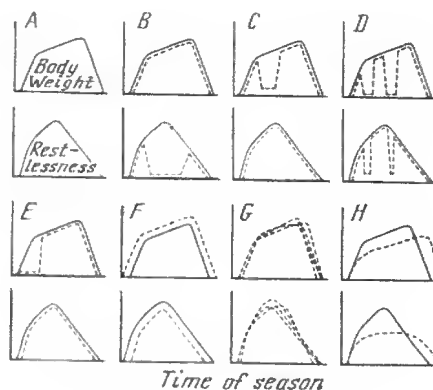
ments – C and D – migratory fattening was reduced by temporary starvation (Berthold, 1975, 1976). In the case of moderate starvation, shown in C, there was no influence on the pattern of restlessness. Severe starvation to a strongly depressed body weight, as shown in D, resulted in the cessation of restlessness. But again the subsequent course of body weight as well as that of restlessness in the experimental group was congruent with the control group and appeared to be uninfluenced by this severe experimental treatment. Preventing the birds from fattening at the beginning of the migratory period (E, Berthold, 1977) yielded similar negative results. The same holds true for an experiment with simulated weather conditions (F, Schindler et al., 1981), in which restlessness was almost completely suppressed in the experimental group on 22 completely dark and rainy nights. Except for a tendency of the experimental group to have a somewhat lower overall time of restlessness and a slightly higher mean body weight, both groups showed congruent patterns of restlessness and of change in body weight.

When south-Finnish birds (from 60° N) and south-German birds (from 48° N) were hand-raised in light conditions that simulated their own breeding area or in those of the other population, all four groups of experimental birds showed almost identical patterns of changes in body weight and of restlessness as shown in G (unpublished data). The only alterations of the endogenously controlled patterns of body weight and restlessness were observed when birds were kept in long-term, constant photoperiodic conditions (Berthold et al., 1972). Then, as demonstrated in H, birds in LD 16:8 showed prolonged and flattened migratory patterns compared with those kept in LD 12:12 or 10:14. In agreement with all earlier findings, and also with those of a very recent experiment, there were no detectable influences on the migratory patterns (unpublished data) when conditions that birds would encounter when landing in the Sahara desert were simulated.

From this set of experiments it seems that, at least in the garden warbler, the patterns of migratory disposition, expressed by changes body weight changes due to fattening, and of migratory restlessness, are under extremely rigid endogenous control. Consequently, a direct and strict genetic basis for the control of these patterns appears most probable. According to these results the patterns are assumed to be innate and highly heritable (e.g., Jacobs, 1981), and with a sliding setpoint (e.g., Mrosovsky, Powley, 1977) that obviously determines the appropriate values.

## GENETIC CONTROL OF THE AMOUNT AND PATTERN OF MIGRATORY RESTLESSNESS

Encouraged by the results obtained from the experiments summarized in Fig. 1, we planned a long-term experiment to test the hypothesis of an innate character in the amount and pattern of migratory activity. For experiments of this type the blackcap, Sylvia atricapilla, a widespread species with marked geographical and ecological differentiation, appeared most suitable. We first considered whether populations of this species showed varying amounts of migratory restlessness in relation to the migratory distances as found in comparisons among species. Such species differences have been shown in both earlier and more recent experiments for eleven species of the genus Sylvia (e.g., Berthold, 1982, unpublished data). The question concerning different populations is answered by the data given in Fig. 2 A, B. We hand-raised nestlings of three populations of European blackcaps and one African population. All birds were initially raised in identical simulated natural-light conditions and their migratory restlessness was later measured in all birds under LD 12.5:11.5. The results obtained are in accordance with the distances of migratory flight in the free-living populations which gradually decrease with populations from north to south. The degree of migratory restlessness was, as the patterns of restlessness show, greatest in the Finnish birds, and progressively less in the German, French, and African birds.

To test the hypothesis of innateness of migratory behaviour with respect to amount and pattern, cross-breeding was considered the most appropriate method. If the expression of migratory restlessness is under direct genetic control, it is logical to assume a polygenic basis. An intermediate expression of restlessness in both amount and pattern in hybrids from two parental populations, which are differentiated by their restlessness, might then be expected (e.g., Berthold, Querner, 1981).

For our cross-breeding experiment we used the birds from which the data presented in Fig. 2 A, B derived. We choose, for practical reasons, the African and German birds as parental stocks. We successfully hand-raised 32 hybrids and used the same methods to record their migratory restlessness as had been used for their parents (Berthold, Querner, 1981). The results are shown in Fig. 2 C, D. As one sees, amount as well as pattern of the restlessness of the $F_1$-hybrids are clearly intermediate in comparison to the parental populations. Thus amount and pattern of migratory restlessness in the blackcap are shown to be under direct and obviously strict genetic control. With these findings in mind it is no longer surprising that the pattern of restlessness in the even more typical migratory garden warbler proved highly insensitive to various environmental influences (Fig. 1).

## THE GENETIC CONTROL OF MOULT IN MIGRANTS

While performing the cross-breeding experiment with blackcaps described above we planned to include a study of juvenile development, including moult, and of morphological features associated with migration: wing length and body weight.
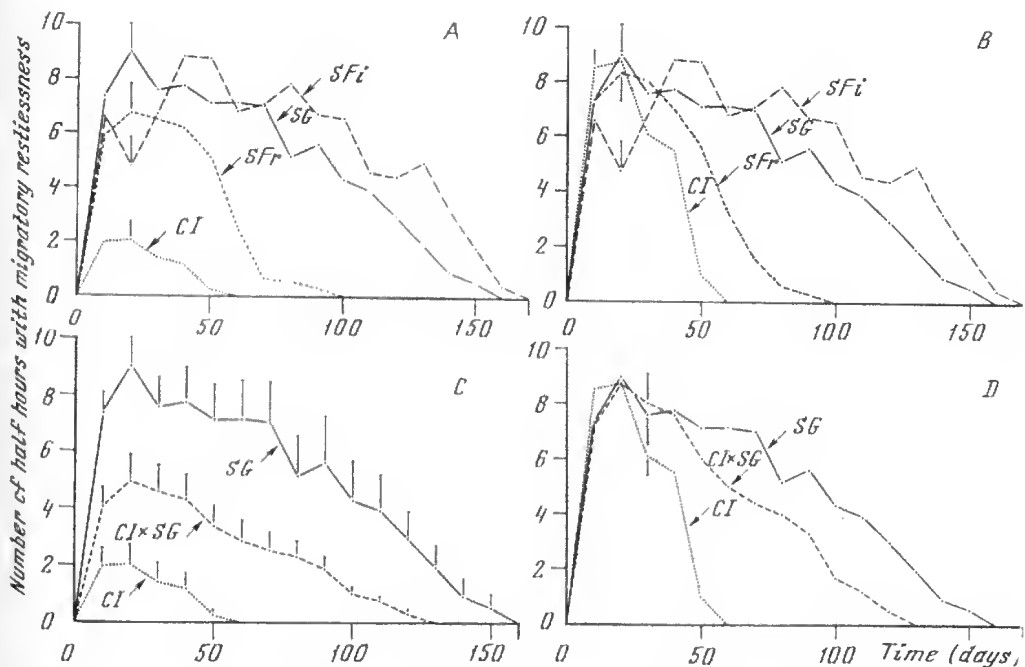
F i g. 2. A and B – temporal course of migratory restlessness of groups of
Sylvia atricapilla from three European and African populations. SFi – sou-
thern Finland; SG – southern FRG; SFr – southern France; CI – Canary Isl-
ands; Africa. A – data for all the birds in each group. B – data for only
those birds that showed restlessness. C and D – time course of migratory
restlessness of hybrids (CI x SG) compared with that of the SG and CI st-
ocks SG and CI. C corresponding with A, D corresponding with B (for det-
ails, see Berthold, Querner, 1981)

As known from earlier studies with Sylvia species, moult starts at an
earlier age and is of shorter duration in more migratory species than in more
resident species (e.g., Berthold et al., 1970). Since migratory performance
in the chosen blackcap populations decreases from north to south, north to
south differentiations in the moult as mentioned were to be expected.

Fig. 3 A shows the mean durations of juvenile moult including their stand-
ard errors for Finnish, German, French, and African birds. Indeed, there was
a progressively later onset of moult in populations from north to south.
That a difference in the duration of the moult occured only between German
and Finnish birds and not with French and African birds has the following
reason: French and African birds had already been transferred to constant
LD 12.5:11.5 conditions before the onset of their moult. In these birds the
relatively short day length of 12.5 hours therefore had a comparably higher
accelerating effect on the subsequent course of their moult than in the
other experimental groups (e.g. Berthold et al., 1970).

Fig. 3 B shows the result of the cross-breeding experiment: the time
course of the juvenile moult of the $F_1$-hybrids was an intermediate between
that of the parental populations. All differences in onset, duration, and

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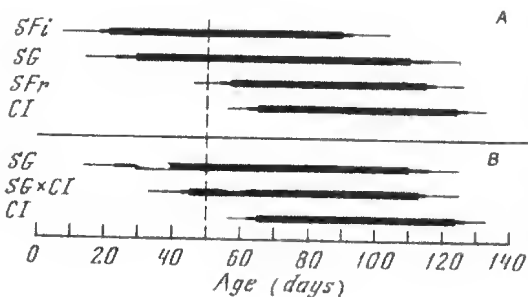
F i g. 3. A — temporal course of juvenile moult of four populations of Sylvia atricapilla with standard errors for the duration of molt. B — data from hybrids and their parental stocks. Abbreviations as in Fig.2; for details see Berthold,Querner, 1982 a

termination were statistically significant except the termination of hybrid moult compared to that of the German parents.

This result is in agreement with earlier findings when garden warblers of different populations were raised in various environmental conditions and showed a population-specific juvenile development regardless of the conditions. These and our recent results of the cross-breeding experiment indicate that the time course of juvenile development in its adaptedness to varying migratory performance is under direct and obviously strict genetic control (Berthold, Querner, 1982a).

THE GENETIC CONTROL OF WING LENGTH AND BODY WEIGHT IN MIGRANTS

Four years ago in Nature Boag and Grant (1978) wrote: "Ecologists use measurements of avian morphological characters to test and modify evolutionary theories. But virtually nothing is known about the inheritance of such characters..." Physiologists, among others, I would like to add, behave the same way."

In the meantime, the situation has improved insofar as some indirect or tentative approaches, since, for example, calculations of heritabilities in feral populations have led to more or less convincing evidence that these characters were highly heritable (e.g., Boag, Grant, 1978). The approaches, however, left some uncertainties as Boag and Grant wrote: "The tests do not eliminate the possibility of genotype-environment interactions or correlations, but ... reduce the likelihood of the most obvious biases. There remains the possibility that the values are inflated by genotype-environment correlations and interactions."

Doubtless, cross-breeding experiments, performed in defined conditions, provide the most reliable results concerning the genetic basis of morphological characters associated with migration. Since various blackcap populations vary conspicuously with respect to wing length, wing shape and body weight (Fig. 4), instructive results from our cross-breeding experiment could be expected. As Fig. 4 shows, the German and African parental populations differ in fat-free premigratory body weight by about two grams and in wing length by about three millimeters. The data obtained from 33 $F_1$-hybrids are intermediate. This intermediacy indicates their direct genetic basis and produces phenology very similar to, or even undistinguishable from, those of feral southern French blackcaps (Berthold, Querner, 1982a).

F i g. 4. Premigratory body weight and wing length (mean values and standard errors) of four populations of _Sylvia atricapilla_ and of hybrids. Abbreviations as in Fig. 2; for details see Berthold, Querner, 1982a
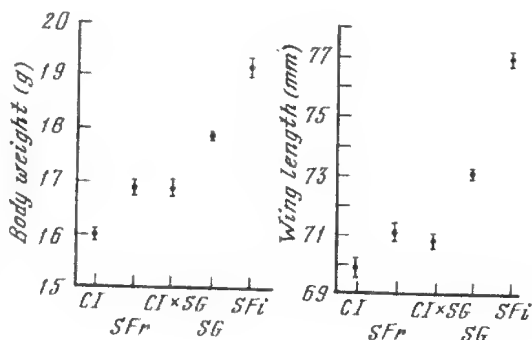


## POLYMORPHISM AS A CONTROLLING SYSTEM OF PARTIAL MIGRATIONS: THE INNATENESS OF THE MIGRATORY URGE

With respect to the control of partial migration in birds there are two controversial hypotheses: Lack (1943) proposed, mainly on the basis of ringing recoveries, a genetic determination of migrants and residents, i.e. a polymorphism, or, in this special case, a dimorphism. Kalela (1954), on the other hand, hypothesized a behavioral-constitutional control mechanism with a facultative determination of migratory behaviour. According to his opinion, during autumnal territorial fights losers should be forced to leave the breeding area as migrants whereas winners should be able to remain as residents.

While investigating the migratory restlessness of Mediterranean warblers and blackcaps of three European populations and one African population (Berthold, 1974, 1978), we obtained the first experimental evidence for the control of partial migration. The findings supported Lack's hypothesis in that the development of restlessness of experimental groups in constant experimental conditions was a fairly good reflection of the typical and partially migratory habits of the feral populations. Thus, the different migratory habits seemed to be endogenously preprogrammed or innate.

The next and more conclusive evidence resulted from the cross-breeding experiment with African and German blackcaps as treated above. Here, the percentage of birds displaying restlessness increased from 23 to 56 from the African parental birds to the $F_1$-offspring, i.e. from one generation to the next, when the poorly migratory African birds were cross-bred with the exclusively migratory German blackcaps. The most plausible explanation for this finding is that an introduction of genes causing migratory restlessness from the German parents increased the proportion of migratory individuals in the $F_1$-hybrids or, in other words, that the migratory urge is innate and heritable.

To test this explanation we started an inbreeding experiment with southern French blackcaps in 1977 (Berthold, Querner, 1982b). In a large sample of 102 experimental individuals from this population, known to be partially migratory, we found that 77% displayed migratory activity whereas 23% did not. Assuming polymorphism (or dimorphism in this special case) is the basis of this migratory habit, inbreeding the migrant and nonmigrant morphs should conform with three predictions: the offspring of pairs of migrants should

show an increase in the ratio of migrants to nonmigrants compared with the original population and to the offspring of pairs of nonmigrants. Similarly the offspring of pairs of nonmigrants should show an increased fraction of nonmigrants compared with the original population. Up to 1981, we successfully raised 39 birds of the $F_1$-generation and investigated their migratory activity in the same way as had been done earlier with the parental birds. The data obtained fulfilled two of the three predictions mentioned above (Table 1): the offspring of the nonmigrants showed a significant (30%) increase in the number of nonmigrants compared with the parental population. The ratio of nonmigrants to migrants was also significantly different from the offspring of migrants. Moreover, although not statistically significant, there was also some evidence in favour of the third prediction: the number of migrants in the offspring of pairs of migrants was 8% greater than in the parental population.

The results of this study demonstrate that in the investigated partially migratory blackcap population, the characters "migratory" and "nonmigratory" are heritable and thus establish polymorphism as a controlling system of partial migration for the first time in birds.

In addition to our results, two other collaborators in our institute obtained similar findings in an inbreeding experiment with European Robins, Erithacus rubecula, and in rearing the offspring from either migratory or nonmigratory Blackbirds, Turdus merula, respectively. Thus polymorphism may be a general genetic mechanisms in partial migration.

In light of recent findings of van Noordwijk et al. (1981), that the timing of reproduction in the great tit Parus major may change genetically with rates of up to one week per five generations, polymorphism of partial migration appears as a possibly highly adaptive feature. When cross-breeding and inbreeding our Blackcaps, as demonstrated above, produced alterations in the percentages of migrants and nonmigrants from one generation to the next in the magnitude of about 30%, it implicates the possibility that under high selective pressures a partially migratory population should be able to shift on a genetic basis to (almost) exclusively migratory or nonmigratory within a relative small number of generations. We have started relevant experiments to investigate this highly exciting question.


T a b l e   1. The ratio of migratory active and inactive individuals in a partially migratory population of Sylvia atricapilla and in two inbred strains of migrants and nonmigrants (for details, s. Berthold, Querner, 1982b)

| | Original partially migratory population | $F_1$-individuals from pairing nonmigratory x nonmigratory birds | $F_1$-individuals from pairing migratory x migratory birds |
|---|---|---|---|
| | n = 102 | n = 19 | n = 20 |
| number of migratory active individuals | 79 | 9 | 17 |
| number of nonmigratory individuals | 23 | 10 | 3 |

$p < 0,01$   $p < 0,025$

SUMMARY

In Figure 1, data compiled from eight experiments on the garden warbler show that the endogenously expressed patterns of migratory fattening and of migratory restlessness of the first autumnal migratory period are highly insensitive to environmental influences. In the Blackcap, in which the amount of restlessness differs between populations according to the migratory distances, a cross-breeding experiment showed that the amount and pattern of restlessness are under direct and obviously strict genetic control. The same cross-breeding experiment demonstrated also a direct genetic basis for the time course of the juvenile moult in its adaptation to the population-specific migratory period, and for two morphological features associated with migration - body weight and wing length. In an inbreeding experiment with strains of with and without migratory behavior from a partially migratory Blackcap population it was shown that migrants and nonmigrants were genetically determined morphs in a (balanced) polymorphism (dimorphism). The alteration of the ratio of migrants to nonmigrants by about 30% from the parental to the $F_1$-generation suggests a potentially high evolutionary rate of migratory behaviour under high selection pressures. These results support the view that migratory behaviour in typically migratory birds is to a high degree the outcome of endogenous programs and that typical migrants are largely preprogrammed "automats".

R e f e r e n c e s

Berthold P. - In: Circannual clocks / Ed. by E.T.Pengelley. N.Y.; L.: Academic Press, 1974.

Berthold P. - Naturwissenschaften, 1975, 62, p. 399.

Berthold P. - Vogelwarte, 1976, 28, p. 263-266.

Berthold P. - Vogelwarte, 1977, 29, p. 113-116.

Berthold P. - Experientia, 1978, 34, p. 1451.

Berthold P. - In:Acta 17 Congr. Internat. Orn. Berlin, 1980, p.473-482.

Berthold P. - Orn. Fennica, 1982.

Berthold P., Gwinner E., Klein H. - Vogelwarte, 1970, 25, p. 297-331.

Berthold P., Gwinner E., Klein H., Westrich P. - Z. Tierpsychol., 1972, 30, p. 26-35.

Berthold P., Querner U. - Science, 1981, 212, p. 77-79.

Berthold P., Querner U. - Experientia, 1982a, 38, p. 801-802.

Berthold P., Querner U. - Experientia, 1982b, 38, p. 805-806.

Boag P.T., Grant P.R. - Nature, 1978, 274, p. 793-794.

Gwinner E. - Naturwissenschaften, 1974, 61, p. 405.

Gwinner E. - In: Handbook of behavioral neurobiology. Vol. 4 / Ed. by J.Aschoff. New York: Plenum Press, 1981, p. 381-389.

Jacobs J. - Z. Tierpsychol., 1981, 55, p. 1-18.

Kalela O. - Ann. Zool. Soc. Vanamo, 1954, 16, p. 1-30.

Lack D. - Brit. Birds, 1943/44, 37, p. 122-130, 143-150.

Mrosovsky N., Powley T.L. - Behavioral Biol., 1977, 20, p. 205-223.

Noordwijk A.J. van, Ballen J.H. van, Scharloo W. - Oecologia, 1981, 49, p. 158-166.

Schindler J., Berthold P., Bairlein F. - Vogelwarte, 1981, 31, p. 14-32.

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PHOTOPERIODIC CONTROL OF POSTJUVENILE
AND POSTNUPTIAL MOLTS IN PASSERIFORMES

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Although the role of photoperiodic regulation of breeding activity has
been well documented (Farner, 1964; Wingfield, Farner, 1980), the influence
of daylength on molting requires further consideration. Apparently the
earliest scientific investigation of control of molt was the work of Miyaza-
ki (1934). Considerable light was shed on the problem by the research of
V.F.Larionov (1941, 1945, 1957). The theoretical concept developed by Wolf-
son (1954, 1965, 1970) of photosensitive phases in the annual cycle, furthe-
red understanding of the role of photoperiod in control of molt. The main
conclusion that can be drawn from these investigations is that shortening
daylength in the fall decreases the duration of the molting process.

The research carried out in Leningrad State University was designed to
illuminate the characteristics of photoperiodic control in various passerine
groups, as well as to work out general principles of control of molt appli-
cable to this order (Noskov, Siletsky, 1969; Noskov, 1975, 1977, 1978; Rym-
kevich, 1976a,b, 1977; Noskov, Rymkevich, 1977, 1978; Noskov, Smirnov, 1979;
Gaginskaya, Noskov, 1981). The effect of various daylengths on members of 42
species of the following families have been analyzed: Alaudidae, Motacillidae,
Turdidae, Sylviidae, Muscicapidae, Paridae, Emberizidae, Fringillidae, Plo-
ceidae and Sturnidae.

The analytical methods applied to the molting process revealed not only
the presence or absence of this process, but also allowed characterization
of its rate, extent, and duration of shedding and growth on all feather
tracts.

For all species investigated it was found that photoperiodic control can
affect the rate of molting.

Experiments showed that this occurs in two ways: a) the growth rate of the
feathers themselves changes, or b) the number of feathers molting simulta-
neously changes.

Change in the rate of feather growth was found in only a few groups, no-
tably in the Fringillidae. Thus, growth of the third and fourth primaries in
Chloris chloris was completed in 12-16 days on LD 14:10, whereas on LD 18:6
22-26 days were required. It was discovered that the growth rate of feathers
being replaced at the beginning of the molt would increase on longer days
than that of feathers being replaced at the end of the molt. That is,plumage
being replaced in the last stages of the molt, in order to grow in at the
place observed in the first stages, requires shorter days.

In almost every species the shedding of old feathers depends on photope-
riodic conditions during both postjuvenile and postnuptial molts. It was
found that on longer days shedding proceeds with lesser intensity and the
whole process extends over a longer period of time (Fig. 1, A, B). If each
successive stage of the molt is accompanied by shortening daylengths, the
overall intensity of the process remains constant. Therefore, if birds are
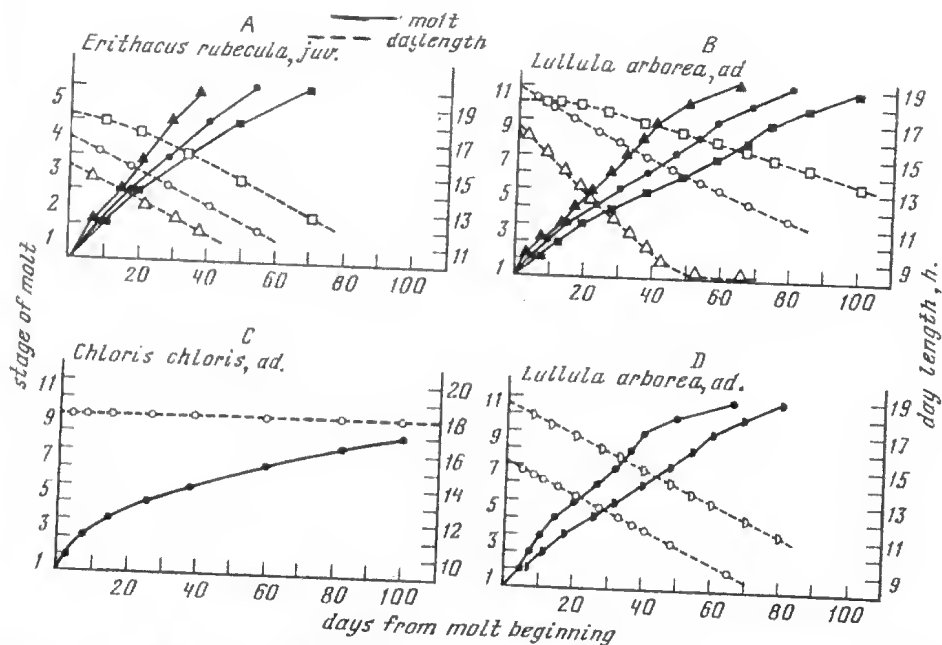
F i g. 1. Dependens of the rate of postjuvenile (juv) and postnuptial (ad) moults on photoperiodic conditions in different species. Geometrical shape indicates the conditions and results in given experimental groups

exposed to a fixed photoperiod, the rate of shedding decreases considerably towards the end of the molt, and the whole process is unnaturally drawn out, or even halted completely.

The following question arises: What constitutes the deciding factor in control of molt - the rate of shortening of days, or daylength itself? Experiments in which birds were subjected to light regimes that changed at an equal rate but differed in absolute levels of daylength revealed, that the organism responds to absolute daylength. When the range of daylengths was shorter overall, plumage was shed more rapidly and the whole molting process was effected more rapidly.

Thus, the results of these experiments indicate that control of molt is exerted on every stage of the process. Each phase, regulated by a reaction to photoperiod, presents a certain requirement of daylength. The beginning phases need longer days, whereas the final stages require shorter days. Therefore, for representatives of a given geographical population, molting proceeds normally only within a certain interval of daylengths to which the birds are adapted. The shorter the daylength within a photoperiodic interval, the more intensively the given phase of molting progresses. It is suggested that this aspect of photoperiodic control be referred to as "stage-by-stage" regulation of the molting process.

Adaptation of the molting process to specific photoperiodic conditions and the existence of a photoperiodic interval with upper and lower thresholds means that the onset of the molt, as well as its completeness, can be controlled by daylength.

931

Parus major, juv
LD 19:5 → 14:10     LD 16:8 → 11:13

F i g. 2. Completeness of postjuvenile moult of Great Tits in various
photoperiodic conditions: 1 - new plumage, 2 - old plumage

It has been shown experimentally that a significant shortening of dayl-
ength beyond a lower threshold causes the molt to cease. In nature, this
occurrence is not uncommon in the Paridae and Fringillidae, If the daylengths
become too short, a postnuptial molt late in the season, ceases completely
in the concluding phases, so that the plumage will then include old feathers
that otherwise would have been replaced late in the molt.

For many species, during postjuvenile molt accelerated shortening of
daylength may decrease the proportion of plumage replaced not only at the
expense of those feathers shed at the end, but also those shed in the middle
of the process (Fig. 2). The adaptive significance of this is to decrease the
overall time in molt and insure timely progression on to migration or to
wintering conditions.

The upper threshold of daylength for the postjuvenile molt in many species
is determined by the age of the bird when the molt begins. The lower the ab-
solute level of this threshold, the greater the influence of photoperiodic
conditions on the onset of the molting process. This is especially true for
Chloris chloris, Spinus spinus, Fringilla coelebs, Emberiza citrinella,
Erithacus rubecula, and other species with two reproductive periods in one
breeding season. Photoperiod plays a lesser role in instigating postjuvenile
molt among single-clutch species such as Emberiza hortulana, Coccothraustes
coccothraustes, Sylvia communis and Sylvia curruca. Thus, for Emberiza cit-
rinella the maximum age at which molting can begin under maximum daylength
for that species is 60 days. This critical age is determined by genetic, en-
dogenous rhythms and cannot be increased by increasing daylength, although
age of onset of molt can be reduced to 20 days by reducing daylength. For
Emberiza hortulana, the maximum age at which molting may begin is 25 days,
the minimum is 18 days. Thus, the possibility of shifting the initial   molt-
ing period by photoperiodic regulation spans 40 days in the first case, and
only 7 days in the second (Fig. 3).

Finally, for such single-clutch species as Sylvia borin, Ficedula hypoleu-
ca and a few others, photoperiod can under no circumstance change the period
during which the molt is initiated because this period has already been set
at the earliest possible age by endogenous factors.

The onset of postnuptial molt, to an even greater degree than that of the
postjuvenile molt, depends on endogenous rhythms. For the majority of species
studied postnuptial molt is coupled with the end of breeding activity. For
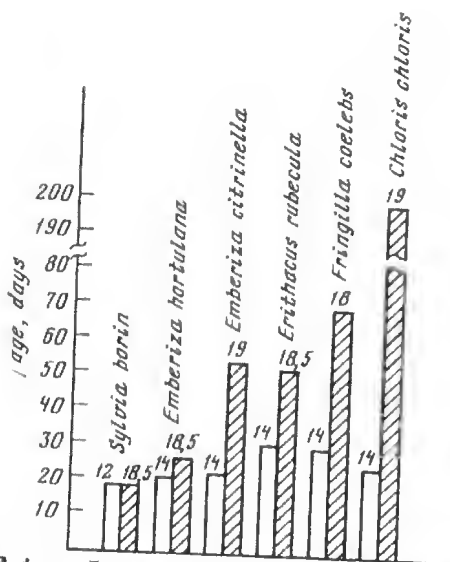
F i g. 3. Age at onset of postjuvenile molt in various photoperiodic conditions. Figure – durations of daylegth in hours

F i g. 4. Onset of postnuptial molt (arrows), taking place in nesting area, in various photoperiodic regimes during the period of breeding activity. Figure – durations of daylength in hours
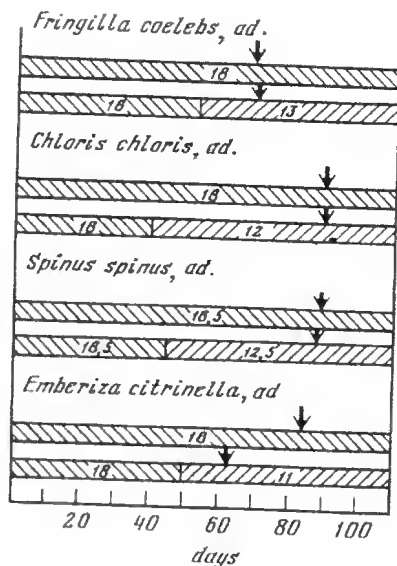
F i g. 5. Onset of postnuptial molt (arrows), taking place in wintering area, in photoperiodic regimes subjected to decreasing day – length at various seasons
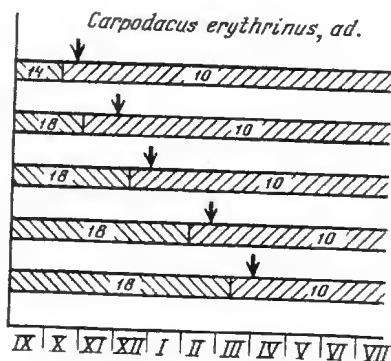
this reason, the period in which molting begins is often determined by the duration of breeding activity. This type of indirect control over onset of molting is found in Lullula arborea, Ficedula hypoleuca, Parus major, Fringilla coelebs, Carduelis carduelis, Acanthis flammea, Chloris chloris, Spinus spinus, Pinicola enucleator, Coccothraustes coccothraustes and Loxia pityopesittacus. Only in Emberiza citrinella was it possible to shift the onset of molt back by shortening daylength during breeding activity (Fig. 4). Among those species that undergo molt in their wintering areas, Carpodacus erithrinus and Emberiza aureola were investigated. In these two species the onset of postnuptial molt did not depend on the duration of breeding activity. Here, the exclusive regulating factor was daylength (Fig. 5).

The material presented demonstrates that the fundamental aspect to be considered in photoperiodic control of molt is the stage-by-stage nature of

its regulation. It is proposed that 1) the rate of molting is under photoperiodic control for the entire duration of the process; 2) each successive stage, as well as the molting process in its entirety, is adapted to a given set of photoperiodic conditions - the photoperiodic interval - within which the molt proceeds normally; 3) photoperiodic requirements in the process of the molt undergo a progressive change with each successive stage reacting to a span of shorter daylengths; 4) the rate of plumage replacement at each stage depends on the absolute levels of daylength within the photoperiodic interval - the shorter the days, the faster the replacement rate; 5) the rate of plumage replacement changes according to the extent to which old feathers are shed simultaneously, and also the rate at which new feathers develop.

Thus, stage-by-stage regulation serves as a mechanism by which the molting process can be completely interrupted or significantly slowed down if the length of the day exceeds or does not reach the thresholds of the photoperiodic interval, within which the rate of the molting process is controlled.

R e f e r e n c e s

Farner D.S. - Amer. Sci., 1964, 52, p. 132-156.
Gaginskaya A.R., Noskov G.A. - In: Polevoi vorobei. Leningrad, 1981, p. 84-90.
Larionov V.F. - Dokl. AN SSSR, 1941, 32, p. 227-229.
Larionov V.F. - Uch. zap. Moskovskogo Univer., 1945, 88. 95 p.
Larionov V.F. - Dokl. AN SSSR, 1957, 112, p. 779-781.
Miyazaki H. - Tohoku Imper. Univ. Sci. Rep., 1934, 4, p. 183-203.
Noskov G.A. - In: Issledovania produktivnosti vida v areale. Villnius, 1975, p. 106-117.
Noskov G.A. - Zool. Journ., 1977, 56, p. 1676-1686.
Noskov G.A. - Ekologia, 1978, 1, p. 61-69.
Noskov G.A., Rymkevich T.A. - In: Metodiki issledovania produktivnosti i struktury vidov ptits v predelakh ikh arealov. Villnius, 1977, p. 37-48.
Noskov G.A., Rymkevich T.A. - Vestn. Leningr. Univ., 1978, 9, p. 12-22.
Noskov G.A., Siletsky V.V. - In: Ornitologia v SSSR. Ashkhabad, 1969, 2, p. 456-459.
Noskov G.A., Smirnov E.N. - Biolog. Nauki, 1979, 3, p. 38-45.
Rymkevich T.A. - Vestn. Leningr. Univ., 1976, 15, p. 19-25.
Rymkevich T.A. - In: Materialy VII Vsesoyusnoi ornitologicheskoi konferentsii I, 1977, p. 154-155.
Savinich I.B. - Vestn. Leningr. Univ., 1983, 21, p. 19-25.
Wingfield J.C., Farner D.S. - Prog. Roprod. Biol., 1980, 5, p. 62-101.
Wolfson A. - J. Exp. Zool., 1954, 125, p. 353-376.
Wolfson A. - Arch. Anat. microsc. Morphol. exper., 1965, 54, p. 579-600.
Wolfson A. - Coll. Intern. CNRS, 1970, 172, p. 93-112.

# ENDOCRINE CORRELATES OF MOLT AND REPRODUCTIVE FUNCTION IN BIRDS

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## INTRODUCTION

Under natural conditions the majority of species of birds is known to exhibit annual cycles that affect both physiological and behavioral manifestations. It seems clear that, during the course of evolution, the programming of biological rhythms in accordance with bioclimatic seasonal cycles has resulted in optimal adaptation of individuals and of species to varying environments, and hence to improved chances for survival and reproduction. Thus seasonal occurrence of basic processes such as reproduction, molt and migration is exactly timed with environmental conditions. A long series of experiments has demonstrated the synchronizing role played by external factors in connection with these functions. But optimal programming of the most important biological functions also means that exact temporal relations must be maintained between these different events, which, in general, never take place simultaneously due to their high energy requirements, or simply for obvious reasons of efficiency (e.g. molt and migration). In the majority of migratory species, reproduction, molt and migration thus follow a strict sequence spread out over the year.

Regarding the particular relationships between reproduction and molting, which the present contribution will consider, the direct correlation observed in most species between the onset of molt and the end of the breeding season has been emphasized many times (Lincoln et al., 1980; Mewaldt, King, 1977; Schreiber, 1980). Moreover, from a series of studies based on various categories of age, sex and breeding status, the concept has emerged that the timing of the onset of molt is dependent on the intensity of breeding activity (Dhont, Smith, 1980; Dittami et al.,1979; Sealy, 1979; Zwickel, Dake, 1977). If, in a few selected species, breeding and molt may overlap to some extent, it is generally assumed that this particular pattern merely stems from circumstantial reasons, such as a very limited time and energy budget available for successful reproduction, molt and preparation for migration within favorable environmental conditions (Cooper, 1975; Foster, 1975; Orell, Ojanen, 1980; Samson, 1976).

For obvious reasons, partial overlap of molting and migration appears much more exceptional(Payne, 1972), since the replacement of flight feathers spans the entire period of postnuptial complete molt (Snow, 1967). However a few such cases have been reported in some short-distance migrant species, like the blue grouse, _Dendragopus obscuras_, - which incidentally migrates largely on foot (Lance, 1970) - and several species of dunlins (Ferns, Green, 1979).

Although many aspects of the complex mechanisms by which external factors may interplay with internal factors to synchronize the phase relationships between reproductive and molt cycles are still obscure, a leading role has been atributed to the annual cycle in daylength. The stimulating role of long days on gonad activation is well known in a large variety of birds in both temperate and tropical regions (review in Farnsr,1970). It has also been

suggested that there is a "long day" requirement for the onset of molt (Assenmacher, 1958; Chilgreen, 1978; Dolnik, 1975; Farner et al., 1980; Verbeek, 1979), irrespective of the exact mechanism that induces it (Berthold, 1979; Dolnik, Gavrilov, 1980; Farner, Gwinner,1980; Lewis et al., 1974; Zwickel, Dake, 1977).

In addition to the primordial role of the annual cycles of the photoperiod in the control of molt, a supportive role may be played by ambient temperature (Chilgren, 1978; Lewis, Farner, 1973) or seasonal variations in humidity (Frith, Carpenter, 1980; Smith, 1978; Maclean,1973; Morel, 1973; Morton, Welton, 1973; Orel, Ojanen, 1980; Payne, 1980).

On the other hand, much less attention has been paid to the annual variations in the complex hormonal balance that may afford another set of enlightening clues for the understanding of both the mechanism of molting and its integrated timing among other biological cycles. The present contribution intends to discuss several salient findings based on hormonal measurements, in addition to morphological data discussed earlier (see Assenmacher, 1958).

INTERRELATIONSHIPS BETWEEN ANNUAL SEXUAL AND THYROID CYCLES

Thyroid hormones have long been known to control the development of skin and its derivatives (Gorbman, 1963) and earlier studies indeed pointed to the thyroid gland as a possible regulator of avian molt (see Assenmacher, 1958; Payne, 1972). However, from a series of recent measurements of annual cycles in thyroid-hormone availability in relation to the sexual cycle, the concept evolved of precise interaction between both endocrine cycles as one basic concept of the sequential occurrence of reproduction and molting.

With respect to the temporal relationships between the annual sexual and thyroid cycles, two patterns have been described: (1) In a few species, thyroid activity is high throughout the reproductive season, e.g., cape cormorant, Phalacrocorax capensis (Berry et al., 1970); migratory Canada goose, Branta canadensis (John, George, 1978); and lesser snow goose, Chen hyperborea (Campbell, Leatherland, 1980), although in the two latter species plasma concentrations of either thyroxine ($T_4$) or triiodothyronine ($T_3$) remain elevated through the subsequent postnuptial molt. (2) More frequently, however, the annual thyroid cycle does not parallel the sexual cycle. Instead, depressed thyroid activity prevails throughout reproduction and increased thyroid activity exists during molt and sexual quiescence, e.g., spotted munia, Lonchura punctulata (Chandols, Thapliyal, 1974), or thyroid secretion displays a clearcut peak immediately after reproduction has ceased. The three species studied in our research group conform to this most common pattern: The Peking duck, Anas platyrhynchos, and teal, Anas crecca (Assenmacher, Jallageas, 1980a; Jallageas et al., 1978; Jallageas et al., 1978), and the emperor penguin, Aptenodytes forsteri (Groscolas, Jallageas, Goldsmith, Lelopu and Assenmacher, in press).

In southern France (latitude 43°38N) Peking ducks breed from March through May, and display a complete postnuptial molt in June-July. Teal, which normally breed in Siberia (latitude 60°N) and winter in southern France from September to February, were prevented from migrating northwards in winter and studied in a large natural park over one year. Under these conditions, the sexual cycls culminated in May-June while the postnuptial molt

took place in July-August, followed by a partial body feather molt in November-December. For the emperor penguin, the plasma samples used for hormone measurements were collected in Antarctica by Dr.R.Groscolas. These birds have their breeding season from April to November, coping with sxtreme climatic conditions and prolonged starvation. The postnuptial molt thus occurs in December, with two partially overlapping phases of feather synthesis and shedding of the old feathers.

Regarding the cycles in sex steroid hormones and thyroxine in relation to molting, two main features are common to the three species: Firstly, molt takes place at the end of the breeding season and is charactsrized by very low plasma concentrations in testosterone (Groscolas et al., in press; Jallageas et al., 1978b). Thus, in ths Psking duck, testosterone levels fell from $5.7\pm0.6$ ng/ml in April to $0.8\pm0.2$ ng/ml in July. In the same environmental conditions, androgen levels decreased in the tsal from $0.7\pm0.06$ ng/ml in early June to $0.1\pm0.03$ ng/ml in August. In the emperor penguin, maximal plasma concentrations found at the time of copulation in April ($13.4\pm4.4$ ng/ml) also reached minimum during molt ($0.15\pm0.02$ ng/ml). Secondly, an indisputable incrsase in the level of oirculating $T_4$ occurs during molt. In the Peking duck, the maximal level observed in June ($9.4\pm0.9$ ng/ml) represents an increase of 75% over the lowest level observed in January. In the teal, the polyphasic pattern of the $T_4$ cycle conforms with the biphasic molting cycle.The first dramatic elevation in plasma $T_4$ occurred through July increasing from $2.47\pm0.15$ to $4.7\pm0.3$ ng/ml and reached its zenith in August ($5.42\pm0.45$ ng/ml) before decreasing steadily until November. A second significant rise took place in December ($4.96\pm0.57$ ng/ml). While the summer peak in $T_4$ clearly corresponded to the postnuptial molt, the winter peak in plasma $T_4$ might be related to prenuptial molting, but also to the low ambinet temperature. In the emperor penguin, highest plasma concentrations of thyroid hormones were also observed during molt, with the $T_4$ peak occurring during synthesis of the new feathers, while the $T_3$ peak was attained only in the subsequent phase of feather loss.

It is important to note that, aside from the second peak observed in winter among the teal, in all thres species seasonal high levels of thyroid hormones cannot be related to notable variations in environmental factors, which conforms to several earlier statements (Chandola, Thapliyal, 1974; Wilson, Farner, 1960). Clearly, the absence of an increase in $T_4$ and $T_3$ among nonmolting emperor penguins, as compared with molting specimens in the same flock (Groscolas et al., in press), furthsr strengthens the hypothesis of a direct link between the seasonal increase in thyroid activity and molt, rather than environmental conditions. Intsrestingly enough, a similar correlation between elevated thyroid activity and molting was also noted in the wild turkey, Meleagris gallopavo (Burke et al., 1977), the domestic turkey (Scanes et al., 1978), the wild mallard drake, Anas platyrhynchos (Haase, Paulke, 1980), the collared dove, Streptopelia roseogrisea (Peczely, Pethes, 1980) and in the rook, Corvus frugilegus (Lincoln et al., 1980).

In conclusion, undsr natural conditions ths postnuptial molt appears characterizsd by a seasonal imbalancs of the thyroxine/testosterone ratio that thus undergoes a steep increase (Fig. 1). The concept of a probable causal
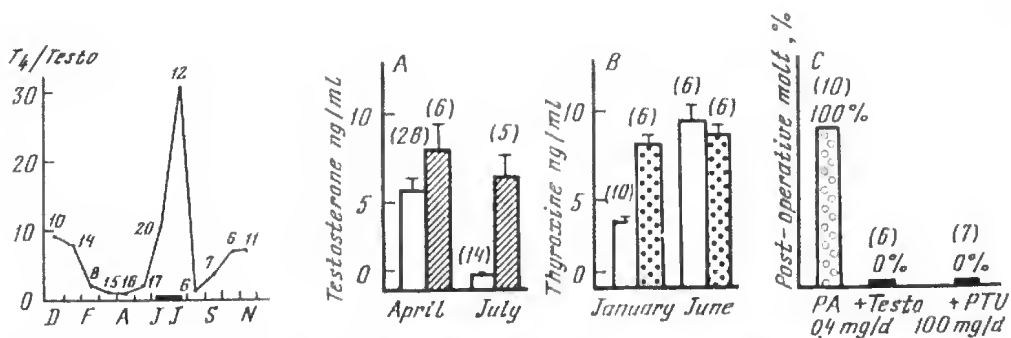
F i g. 1. Annual cycle in the plasma ratio of thyroxine/testosterone in Peking ducks. The horizontal black bar above the abscissa indicates the annual postnuptial molt. Number of birds is indicated

F i g. 2. Implication of testosterone and thyroxine in molt of ducks
A - while surgical thyroidectomy ▨ has no marked effect on plasma testosterone during the breeding season, it prevents the seasonal decline of testosterone and molt in July altogether; B - castration ▨ increases plasma thyroxine in January to maximal levels normally obtained in June (postnuptial molt) and induces body molt. There is no further rise in thyroxine in June; C - whereas ectopic pituitary autografts ▨ lead to testicular atrophy with maintained thyroid function and to a complete molt, it was always possible to prevent the forced molt by treatment with either testosterone or propylthiouracile. Number of birds is indicated in parentheses

link between this hormonal imbalance and the onset of molt receives additional support from a series of experimental data.

EXPERIMENTAL EVIDENCE FOR GONADOTHYROD INTERACTIONS
ASSOCIATED WITH MOLTING PROCESSES
Hormone supplementation or suppression

Experimentally induced hyperthyroxinemia has long been known to induce off-season molting in a variety of avian species (review in Assenmacher, 1958). Recent studies in Peking ducks thus showed that, whatever the reproductive stage, thyroxine treatments mimicking the peak $T_4$ levels normally occurring in June-July depressed testosterone secretion to baseline levels (Jallageas, Assenmacher, 1974).

Conversely, decades ago Zawadowsky and Liptschina (1927) in the domestic fowl, Takewaki and More (1944) in the domestic canary, and Vaugien (1955) in the house sparrow, Passer domesticus, clearly demonstrated that testosterone supplementation obliterated seasonal molting. More recently, testosterone injections monitored to mimick the high androgen levels of the breeding season were shown to depress significantly thyroxine secretion in ducks (Jallageas, 1975; Jallageas, Assenmacher, 1972) and in quail, Coturnix coturnix (Peczely et al., 1980).

On the other hand, surgical thyroidectomy, if performed several months prior to the normal onset of molt, has a blocking effect on molt in ducks (Jallageas, Assenmacher, 1979; Svetsarov, Streich,1940), wild mallard (Haase,
938

1980), domestic fowl (Crew, Huxley, 1927), magpu, _Pica pica_ (Voitkevich, Vasiliev, 1939) and domestic canary (Takewaki, Mori, 1944). Interestingly,under similar conditions, thyroidectomy was also shown to maintain maximal LH and testosterone levels (Fig. 2A) throughout the summer in ducks (Jallageas, Assenmacher, 1979), and to prevent testicular regression in starling, _Sturnus vulgaris_ (Wieselthier, van Tienhoven, 1972; Voitkevich, 1940) and in spotted munia (Thapliyal, Chandola, 1972).

Once again castration had reverse effects and led to a state of permanent molt in the domestic fowl (Benoit, 1929; Finlay, 1925) and in ducks (Caridroit, 1934; Jallageas, Assenmacher, 1979; Streich, Svetsarov, 1936). Additionally, in the latter species castration performed when plasma thyroxine was at baseline levels (late fall) induced a dramatic increase in circulating levels of thyroxine that remained for almost eight months at maximal levels normally measured only during molting (Jallageas, Assenmacher, 1979)(Fig.2B).

Taken altogether,these results clearly demonstrate that in a number of avian species an experimentally induced increase in the thyroxine/androgen ratio - by $T_4$ supplementation of by castration - promotes artificial molting while, conversely, a depressed thyroxine/androgen ratio - by thyroidectomy or androgen supplementation - obliterates the seasonal occurrence of molt.

## Experimental molts

In a series of neuroendocrine studies on the hypothalamic control of pituitary function in drakes, the regular occurrence of a forced and complete molt was noted as an inevitable side-effect of surgical disconnection of the hypothalamus of the anterior pituitary gland, as obtained by autograft of the anterior pituitary onto the kidney (Assenmacher, Baylé, 1968). The dramatic alteration of the endocrine balance resulting from that procedure was characterized by the coincidence of an entirely suppressed gonadal function (Assenmacher, 1958), contrasting with an almost completely maintained thyroid function (Assenmacher, Astier, 1965; Rosenberg et al., 1970). Thus this experimental molt was again associated with a sudden elevation of the relative thyroxine/androgen ratio,and further investigations clearly showed that it could always be completely prevented, by either daily supplementation of physiological does of testosterone (Assenmacher, Baylé, 1968) or by blocking thyroid synthesis with daily administration of propylthiouracile (Baylé, 1972) (Fig. 2C). In the same type of experiment, Novikov, Garmantina and Danilova (1979) recently showed in hens that the well known picture of stress-molting is associated with both a decrease in plasma concentrations of FSH and LH, a resulting arrest of egg-laying and with a state of hyperthyroidism as manifested by an increased PBI.

In conclusion, it thus appears that the concept of a preeminent role of the thyroxine/androgen balance in the control of molting processes adequately conforms with all molting situations, whether in nature or under various experimental conditions.

## Possible impact of thyroid hormones and androgens in molting processes

From early observations on experimental molt and feather growth induced by thyroxine administration, the presumable direct effect of thyroxine on the formation of new feathers has long been postulated (Cole, Reid, 1924, in

the domestic fowl; Hardesty, 1935, in the Guinea fowl, _Numida meleagris_; and Larionov,1931, in the bullfinch _Pyrrhula pyrrhula_). In their remarkable observations, Kraetzig (1937), Svetsarov and Streich (1940) actually showed that from the very first day of thyroxine treatment, a wave of mitoses spread through all feather papillae, together with the neighboring epidermal cells that underwent an intense desquamation. It was concluded that the conjunction of active growth of new feathers and skin desquamation actively led to the shedding of the old feathers.

The data collected from the emperor penguin clearly support this view, since the increased plasma concentration in $T_4$ in molting birds (Groscolas et al., in press) is strongly correlated with a seasonal peak in circulating free amino acids, which, incidentally, is necessary for keratin synthesis (Groscolas et al., 1975). $T_3$, instead, increased in later stages of the molting process, when the old feathers were already shed, and could presumably be associated with increased thermogenesis triggered to compensate for the transient loss of thermal insulation.

Regarding the possible role of androgens in molting processes, it seems reasonable to assume that they firstly account for maintaining a moderate level of thyroid activity during reproduction. Additionally, testosterone has been postulated to exert a direct protective effect on mature feathers (Assenmacher, 1958; Meier, Ferrell, 1978; Payne, 1972; Vaugien, 1955). The recent findings of Wingfield and Farner (1979), who observed concommitantly maintained high plasma levels in testosterone and delayed postnuptial molt in renesting white-crowned sparrows, _Zonotrichia leucophrys gambelii_, may also fit into this hypothesis.

OTHER HORMONAL INTERFERENCES WITH MOLTING

Even if a preeminent role may be assigned to the thyroxine/androgen balance in the induction of molt, a number of other metabolic hormones presumably are associated in that complex mechanism. However, at the present stage, scarce information is available on their possible involvement in molt, apart from a few data on seasonal variations in plasma concentrations of several metabolic hormones during molt.

### Growth hormone (GH)

In this connection, plasma concentrations of GH have been shown to display seasonal variations in Peking ducks and teal (Scanes et al., 1980). Maximal values were observed precisely during the molting period. Additionally, the annual cycles of GH and $T_4$ appeared closely and positively correlated,which, in fact,may result from the stimulatory effect of TRH on GH secretion as has been observed in ducks (Pethes et al., 1979) and the domestic fowl (Harvey et al., 1978). Although Harvey, Scanes, Bolton and Chadwick (1977) showed that acutely heat-stressed chickens had elevated circulating GH levels, it is nevertheless unlikely that the seasonal elevation noted in GH levels of Peking ducks and teal was only linked to high temperature, which in the Mediterranean climate spans several months. On the other hand, enhanced secretion of GH during the molting phase may be related to the concomitant annual peak of serum levels of free fatty acids, described in the Canada goose, and might facilitate thermogenesis in the defeathered bird (John, George, 1977).

## Prolactin (PRL)

No clear statement can be drawn from earlier reports on the possible effects of exogenous administration of PRL on molting, since, depending on authors and/or species, PRL was shown to inhibit or to promote molt, or to have no effect at all on the process (review in Payne, 1972). More recently, Scanes, Sharp, Harvey, Godden, Chadwick and Newcomer (1979), using a radioimmunoassay to measure endogenous plasma concentrations in PRL, actually showed a trend for increased - although not statistically significant - levels of PRL during molt in domestic turkey. As for GH, a concomitant increase in PRL and $T_4$ could indeed result from the stimulatory effect of TRH on PRL as indicated by Peyrot and Vellano (1980). In fact, many more investigations have been undertaken on the possible interactions between PRL and the gonadotropins than between PRL and the thyrotropic system. Inverse correlations were thus observed in a variety of avian species during the annual cycle between plasma concentrations of LH and sex steroid hormones, on the one hand, and PRL on the other (review in Bedrak et al., 1981). These correlations have often been interpreted in the light of Riddle's ancient hypothesis of an antigonadal action of prolactin, although there has been a failure to detect an antigonadal effect of PRL in several species (e.g., Lehrman, Brody, 1961; Gourdji,Tixier-Vidal, 1966; Shani et al., 1973). Finally, it is worth noting than an original trend of investigations proposed that prolactin may have an important role in the determination of various annual metabolic cycles by an annual phase-shift in the diurnal cycle of PRL secretion (Meier et al., 1969) associated with diurnal variations in metabolic responses to PRL (Meier, 1969).

## Corticosteroid hormones

In spite of an ample literature on annual variations in the histology of adrenal cortical tissue in a variety of avian species, with some additional observations on annual cycles in plasma concentrations of corticosterone (review in Assenmacher, Jallageas, 1980b), only a few data appear pertinent to the problem of possible correlations between secretion of corticosteroid hormones and metabolism,and molting processes, However, a detailed comparison of the various parameters of corticosteroid metabolism between molting and breeding drakes has provided interesting results (Assenmacher et al, 1975; Assenmacher, 1980b; Daniel, 1975). In molting birds the secretion rate of corticosterone was slightly increased (+15%), whereas the total plasma concentration in corticosterone was actually decreased (-25%), due to a 50% increase in the metabolic clearance rate of the hormone resulting from the increased levels of $T_4$ prevailing during molt. On the other hand, the plasma concentration of unbound, i.e., biologically active, corticosterone appeared unchanged as compared with the breeding state, since the decrease measured in the total amount of the hormone originated essentially in a lowered synthesis of corticosteronebinding globulin resulting from the concomitantly depressed levels of testosterone. This illustrates not only the occurrence of a complex and variable multihormonal interplay within the endocrine system, but also some major difficulties in the evaluation of a possible adrenal participation in the control of molt. So, although the adrenal gland was secreting more corti-

costerone during molt, no more active hormone was actually available to the target tissues, which, in fact, conforms with the main metabolic trend during molt involving protein anabolism rather than catabolism.

In the same way, reduced levels of corticosterone were also measured in white-crowned sparrows, _Zonotrichia leucophrys gambelii_, during both post-nuptial and postjuvenile molts (Wingfield, Farner, 1978a,b; Wingfield, Smith, Farner, 1980).

### Progesterone

The original statement by Gabuten and Shaffner (1952) that administration of progesterone induced a swift and complete molt in hens was later confirmed by a number of authors (reviews in Assenmacher, 1958; Payne, 1972). However, most recent studies based on the measurement of actual levels of plasma progesterone were unable to assign this hormone any role in the control of molt. Indeed, no significant seasonal changes in plasma progesterone concentrations were noted in wild mallard drakes (Haase, 1980), and no apparent relation between progesterone level and onset of molt was found in the white-crowned sparrow (McCrcery, Farner, 1979). Moreover, lowered levels of progesterone were even found in molting in comparison with laying turkeys and hens (Furr, 1973), although a decrease in actual plasma concentrations can tentatively be ascribed to the stimulatory effect of thyroxine of the metabolic clearance rate of all major steroid hormones (Assenmacher et al., 1975). As for the activating role of administration of exogenous progesterone on molt, it could well be explained by an indirect inhibition secretion of gonadotropins and sex steroid hormones.

### CONCLUSION

If one considers that molt, and more especially the complete postnuptial molt, involves profound alterations in several homeostatic processes, e.g., energy metabolism, both general and a few specific metabolisms of protein, and homeothermia, there can be little doubt that such a complex process requires equally complex hormonal adjustments. At the present stage, however, little is known about the possible implication and precise participation in molting mechanisms of major metabolic hormones such as GH and PRL, not to mention insulin. On the other hand, recent studies have enforced earlier assumptions in favor of the probable role of lowered levels of androgens and increased levels of thyroxine in the onset and completion of molting processes in a variety of avian species. At least in a few selected species submitted to a wide range of experimental schedules, it can be taken for granted that molt is primarily controlled by the annual occurrence of an increased ratio in the plasma concentrations between thyroxine and androgens. Whether this annually recurring hormonal imbalance results directly from external factors rather than from reciprocal interactions between both hormonal systems, the latter being clearly demonstrated in a few species, remains one of the exciting tasks for continued research in this field.

### SUMMARY

The yearly programming of sequentially recurring periods of reproduction, molt and migration appears to result from a complex interplay of seasonal en-

vironmental factors and of multiple hormonal interactions. Among the latter, a series of experimental data including (1) the concomitant measurement of annual cycles in plasma testosterone and thyroid hormones, (2) artificial molts and suppression of annual molting by experimental alteration of the thyroxine/testosterone ratio, and (3) suppression of forced molts by testosterone supply or thyroid blockade, led to the concept of a preeminent role in a number of species of an increased thyroxine/androgen balance in the control of molting processes. The possible implication of further metabolic hormones like GH, PRL, corticosteroids and progresterone is discussed.

R e f e r e n c e s

Assenmacher I. - Alauda, 1958, 26, p. 242-289.

Assenmacher I., Astier H. - Gen. Comp. Endocrinol., 1965, 5, p. 663.

Assenmacher I., Jallageas M. - In: Hormones adaptation and evolution / Eds. Ishii et al. Tokyo/ Berlin: Japan Sciences Societies Press/Springer-Verlag, 1980a, p. 93-102.

Assenmacher I., Jellageas M. - In: Avian Endocrinology / Eds. A.Epple, M.H.Stetson. N.Y.: Academic Press, 1980b, p. 391-411.

Assenmacher I., Astier H., Daniel J.Y., Jallageas M. - J. Physiol. P., 1975, 70, p. 507-520.

Assenmacher I., Bayle J.D. - Arch. Anat. Histol. Embryol., 1968, 51, p. 67-73.

Bayle J.D. - Gen. Comp. Endocrinol., 1972, 18, p. 575.

Bedrak E., Harvey S., Chadwick A. - J. Endocrinol., 1981, 89, p. 197-204.

Benoit J. - Arch. Zool. Exp. Gen., 1929, 69, p. 217-499.

Berry H.H., Millar R.P., Louw G.N. - Comp. Biochem. Physiol., 1979, 62A, p. 879-884.

Berthold P. - Vogelwarte, 1979, 30, p. 7-10.

Burke N.S., Lisiano M.E., Kennamer J.E. - J. Wildl. Manage, 1977, 41, p.650-656.

Campbell R.R., Leatherland J.F. - Can. J. Zool., 1980, 58, p. 1144-1150.

Caridroit F. - C.R. Soc. Biol., 1934, 118, p. 210-211.

Chandola A., Thapliyal J.P. - Gen. Comp. Endocrinol., 1974, 22, p. 184-194.

Chilgren J.D. - Condor, 1978, 80, p. 222-229.

Cole L.J., Reid D.H. - J. Agricult. Res., 1924, 29, p. 285-287.

Cooper J. - Ostrich, 1975, 46, p. 154-156.

Crew F.A.E., Huxley J.S. - Vet. J., 1927, 79, p. 343.

Daniel J.Y. - J. Physiol. P., 1975, 71, p. 132 A.

Dhont A.A., Smith J.N.M. - Can. J. Zool., 1980, 58, p. 513-520.

Dittami J., Kennedy S., Thomforde C. - J. Ornithol., 1979, 120, p. 188-195.

Dolnik V.R. - Zool. Zhur., 1975, 54, p. 1048-1056.

Dolnik V.R., Gavrilov V.M. - Auk, 1980, 97, p. 50-62.

Farner D.S. - In: La Photorégulation de la Reproduction chez les Oiseau et les Mammifères / Eds. J.Benoit, I.Assenmacher. Paris: C.N.R.S., 1970, p. 71-89.

Farner D.S., Donham R.S., Moore M.C., Lewis R.A. - Auk, 1980, 97, p. 63-75.

Farner D.S., Gwinner E. - In: Avian Endocrinology / Eds. A.Epple, M.H.Stetson. N.Y.: Academic Press, 1980, p. 331-336.

Ferns P.N., Green G.H. - Gerfaut, 1979, 69, p. 286-303.

Finlay G.F. - Brit. J. Exp. Biol., 1925, 2, p. 439.

Foster M.S. - Condor, 1975, 77, p. 304-314.

Frith H.J., Carpenter S.M. - Australian Wildl. Res., 1980, 7, p. 117-138.

Furr B.J.A. - Acta Endocrinol., 1973, 72, p. 89-100.

Gabuten A.R., Shaffner C.S. - Poultry Sci., 1952, 31, p. 917.

Gorbman A. - In: Comparative Endocrinology. Vol. 1 / Eds. U.S. von Euler,
    H.Heller. L.: Academic Press, 1963, p. 291-324.

Gourdji D., Tixier-Vidal A. - C.R. Acad. Sci. P., 1966, 262, p. 1746-1749.

Greig-Smith P.W. - Ostrich, 1978, 50, p. 45-58.

Groscolas R., Charpentier C., Lemmonnier F. - Comp. Biochem. Physiol., 1975,
    51B, p. 57-67.

Groscolas R., Jallageas M., Goldsmith A.R. et al. (in press). - In: Proceedings of the IX International Symposium on Comparative Endocrinology / Eds.
    Hong Kong. University Press, 1981.

Haase E. - In: Acta XVII Congressus Internationalis Ornithologici / Ed. by
    R.Nöhring. B.: Verlag der deutschen Ornithologen-Gesellschaft, 1980,
    p. 453-457.

Haase E., Paulke E. - Zool. Anz., 1980, 204, p. 102-110.

Hardesty M. - J. Exp. Zool., 1935, 71, p. 389-416.

Harvey S., Scanes C.B., Bolton N.J., Chadwick A. -I.R.C.S., 1977, 5, p.141.

Harvey S., Scanes C.G., Chadwick A., Bolton N.J. - Neuroendocrinology, 1978,
    26, p. 249-260.

Jallageas M. - J. Physiol. P., 1975, 71, p. 136A.

Jallageas M.,Assenmacher I. - Gen. Comp. Endocrinol., 1972, 19, p. 331-340.

Jallageas M., Assenmacher I. - Gen. Comp. Endocrinol., 1974, 22, p. 13-20.

Jallageas M., Assenmacher I. - Gen. Comp. Endocrinol., 1979, 37, p. 44-51.

Jallageas M., Astier H., Assenmacher I. - Gen. Comp. Endocrinol., 1978a,
    34, p. 68-69.

Jallageas M., Tamisier A., Assenmacher I. - Gen. Comp. Endocrinol., 1978b,
    36, p. 201-210.

John T.M., George J.C. - Arch. Int. Physiol. Biochem., 1977, 85, p. 871-875.

John T.M., George J.C. - Physiol. Zool., 1978, 51, p. 361-370.

Kraetzig H. - Arch Entw. Mech., 1937, 137, p. 86-150.

Lance A.N. - Condor, 1970, 72, p. 437-444.

Larionov W.T. - Arch Entw. Mech., 1931, 124, p. 54-65.

Lehrman D.S., Brody P. - J. Endocrinol., 1961, 22, p. 269-275.

Lewis R.A., Farner D.S. - Condor, 1973, 75, p. 279-286.

Lewis R.A., Farner D.S., King J.R. - Condor, 1974, 76, p. 233-237.

Lincoln G.A., Racey P.A., Sharp P.J., Klandorf H. - J. Zool. L., 1980, 190,
    p. 137-153.

Maclean G.L. - Ostrich, 1973, 44, p. 219-240.

McCreery B.R., Farner D.S. - Gen. Comp. Endocrinol., 1979, 37, p. 1-5.

Meier A.H. - Gen. Comp. Endocrinol. Suppl., 1969, 2, p. 55-62.

Meier A.H., Ferrell B.R. - In: Chemical Zoology Vol. 10 / Ed. by A.H.Brush.
    N.Y.: Academic Press, 1978, p. 213-271.

Meier A.H., Burns J.T., Dusseau J.W. - Gen. Comp. Endocrinol., 1969, 12,
    p. 282-289.

Mewaldt L.R., King J.R. - Condor, 1977, 79, p. 445-455.

Morel M.Y. - Mem. Mue? Nat. Hist. Nat. Paris Ser., 1973, A 78, p. 1-156.

Morton M.L., Welton D.E. - Condor, 1973, 75, p. 184-189.

Novikov B.G., Garmatina S.M., Danilova O.V. - Dokl. AN SSSR, 1979, 247, p. 1000-1003.

Orel M., Ojanen M. - Ornis Scand., 1980, 11, p. 43-49.

Payne R.B. - In: Avian Biology II / Eds. D.S.Farner, J.R.King, K.C.Parker. N.Y.: Academic Prese, 1972,p. 104-155.

Payne R.B. - Ibis, 1980, 122, p. 43-56.

Peczely P., Pethes G. - Acta Physiol. Acad. Sci. Hung., 1980, 56, p.421-430.

Peczely P., Astier H., Jallageas M. - Gen. Comp. Endocrinol., 1979, 37, p. 400-403.

Pethes G., Scanee C.G., Rudas P. - Acta Vet. Acad. Sci. Hung., 1979, 27, p. 175-177.

Peyrot A., Vellano·C. - Gen. Comp. Endocrinol., 1980, 40, p. 318.

Roeenberg L.L., Astier H., Laroche G. et al. - Neuroendocrinology, 1967, 2, p. 113-125.

Samson F.B. - Condor, 1976, 78, p. 505-511.

Scanes C.G., Jallageas M., Assenmacher I. - Gen. Comp. Endocrinol., 1980, 41, p. 76-79.

Scanes G.C., Chadwick A., Sharp P.J., Bolton N.J. - Gen. Comp. Endocrinol., 1978, 34, p. 45-49.

Scanes C.G., Sharp P.J., Harvey S. et al. - Br. Poult. Sci., 1979, 20, p. 143-148.

Schreiber R.W. - Auk, 1980, 97, p. 491-508.

Sealy S.G. - Can. J. Zool., 1979, 57, p. 1473-1478.

Shani J., Furr B.J.A., Forsyth I.A. - J. Reprod. Fertil., 1973, 34, p. 167-170.

Snow D.W. - Br. Truet Ornithol. Field Guide, 1967, N 11.

Streich G., Svetearov E. - Proc. Acad. Sci. SSSR, 1936, 4, p. 157-161.

Svetearov E., Streich G. - C.R. Acad. Sci. SSSR, 1940, 27, p. 392-396.

Takewaki, Mori K.H. - J. Fac. Sci. Imp. Univ. Tokyo, 1944, 6, p. 547-575.

Thapliyal J.P., Chandola A. - Proc. Nat. Acad. Sci. India, 1972, 42B,p.76-90.

Vaugien L. - Bull. Biol. France Belgique, 1955, 139, p.218-244.

Verbeek N.A.M. - Wilson Bull., 1979, 91, p. 420-425.

Voitkevich A.A. - C.R. Acad. Sci. SSSR, 1940, 27, p. 741-745.

Voitkevitch A.A., Vasiliev Yu.A. - Proc. Acad. Sci. SSSR, 1939, 25, p.338-341.

Wieselthier A.S., Van Tienhoven A. - J. Exp. Zool., 1972, 179, p. 331-338.

Wilson A.C., Farner D.S. - Condor, 1960, 62, p. 414-425.

Wingfield J.C., Farner D.S. - Biol. Reprod., 1978a, 19, p. 1046-1056.

Wingfield J.C., Farner D.S. - Physiol. Zool., 1978b, 51, p. 188-205.

Wingfield J.C., Farner D.S. - Gen. Comp. Endocrinol., 1979, 38, p. 322-331.

Wingfield J.C., Smith J.P., Farner D.S. - Gen. Comp. Endocrinol., 1980, 41, p. 372-377.

Zawadoweky B., Liptschina L. - Arch. Entw. Mech., 1927, 113, p. 432-446.

Zwickel F.C., Dake J.A. - Can. J. Zool., 1977, 55, p. 1782-1787.

# ENDOCRINE AND PROTOPERIODIC RELATIONSHIPS DURING PHOTOREFRACTORINESS, POSTNUPTIAL MOLT, AND ONSET OF MIGRATION IN ZONOTRICHIA LEUCOPHRYS GAMBELII

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INTRODUCTION

The annual cycles of many species of birds are synchronized with annual changes in the environment by the use of daylength as predictive information (for reviews, see Dolnik, 1975, 1976, 1980a; Farner, 1964, 1970; Farner, Follett, 1979; Murton, Westwood, 1977; Wingfield, Farner, 1980). Among many smaller species, vernal and autumnal migration are each preceded by a complete or partial molt (e.g., Stresemann, Stresemann, 1966). In such species, the termination of reproductive function, the postnuptial molt, premigratory fattening and onset of migration occur in a species-specific order and are usually temporally separated (Farner, 1964; Farner et al., and Lewis 1980;, Wingfield, Farner,1980).

Although the vernal and autumnal premigratory phases are superficially similar in that each is usually preceded by a molt and premigratory fattening, the former is accompanied by development of the reproductive system, whereas the autumnal migration follows the termination of the reproductive effort with the development of photorefractoriness (e.g., Ferner, Lewis, 1971; Wingfield, Farner, 1980). Although this similarity might suggest a common photoperiodic control mechanism, our recent investigations of Zonotrichia leucophrys gambelii, a typical migratory passerine taxon, suggest that their mechanisms are very different (Farner et al., 1980; Farner et al.,1981).

This difference was initially suggested by comparison of the expression of vernal and autumnal functions under laboratory conditions. The suquence of the vernal events, which is induced directly by increased daylength, can be altered by photoperiodic manipulation. For example, on 20L 4D the prenuptial molt may be coincident with premigratory fattening instead of preceding it (King, 1961) and onset of fat deposition may coincide with that of Zugunruhe instead of preceding it (King, Farner, 1963).

The autumnal sequence of functions is induced only after 40-60 long days, by which time the birds are photorefractory and the gonads are in regression. At least the development of photorefractoriness and the postnuptial molt are independent of the vernal, photoperiodically induced plasma levels of gonadotropins and the development of the testes (Matt, 1982). Also, the development of photorefractoriness is not dependent on testicular hormones (Mattocks, 1982; Mattocks, Farner, Follett, 1976). These observations emphasize the essential independence of the autumnal from the vernal events even though both are induced by long days. The mutual independence of the systems that control the two sequences is also suggested by the observation that intermediate daylengths, such as 12 hours, induce all vernal functions by fail to induce the autumnal functions (Farner et al., 1980).

Unlike the vernal sequence no investigation has yet demonstrated that the natural sequence of autumnal functions can be separated by photoperiodic

manipulation after the onset of photorefractoriness and regression of the gonads, although the rate of postnuptial molt can be increased by reducing daylength.

TWO HYPOTHESES

The observations on Z.l.gambelii presented above suggest two complementary hypotheses of the nature of the photoperiodic mechanism that induces the preparation for autumnal migration in this taxon. The first hypothesis proposes that the late-summer functions are induced by a slow photoperiodic process that culminates with the development of photorefractoriness and the consequent termination of reproductive function. The second hypothesis proposes that the late-summer functions are induced as an internally coupled unit. In this communication we report the results of two experiments that test predictions derived from these hypotheses.

THE EXPERIMENTAL BIRDS

Z.l.gambelii has, in general, the longest migratory route among the races of Z.leucophrys. The principal breeding areas lie in British Columbia, Alaska, and Yukon. The major wintering areas are in California, New Mexico, Arizona, and northern Mexico with isolated populations in central and eastern Washington and Oregon.

The males employed in our experiments were captured from wintering flocks on the Sunnyside Game Refuge in central Washington (46°N, 120°W) from where they were transported to Seattle (48°N, 122°W) where they were held in outdoor aviaries until transferred to constant-condition chambers for the experiments.

THE EXPERIMENTS

In Experiment I first-year males captured in October-November were transferred on 5 December to constant-condition chambers with a photoregimen of 8L 16D, which on 20 December was changed to 12L 12D. Thereafter four groups of 9-12 each were transferred to long days (20L 4D) at four stages of testicular development (Fig. 1), as determined by the examination of the intact testes via laparotomy (cf. Farner et al., 1981) - at the end of the logarithmic phase of growth (ELP, combined testicular weight, ca. 200 mg), at or near maximum testicular weight (MTW, > 250 mg), midway through testicular regression (MTR, ca. 50 mg), and at or near the end of testicular regression (ETR, < 10 mg). As noted above, 12L 12D induces neither photorefractoriness nor postnuptial molt.

The results from Experiment I indicate that all four groups responded with gonadal growth on transfer to long days. This confirms our earlier observation (Farner et al., 1980) that 12L 12D does not induce photorefractoriness and postnuptial molt in Z.l.gambelii. Thus this emberized species differs from Fringilla coelebs in which 12L 12D induces postnuptial molt, premigratory fattening, and apparently photorefractoriness (Dolnik, 1975b, 1976). and from Sturnus vulgaris in which successive gonadal cycles on 12L 12D are accompanied by photorefractoriness and postnuptial molt (Gwinner, Dittami, Ganshirt, 1980). Whether these differences indicate that the photoperiodic systems of these three species have evolved independently, or simply small

Days of 12L 12D
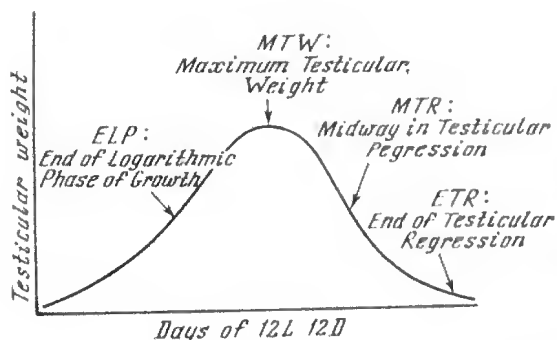
F i g. 1. Schematic representation of the stage of the testicular cycle in which the four groups in Experiment I were transferred from 12L 12D to 20L 4D

adaptive differences in threshold of a common ancestral system, remains to be resolved. However, other differences suggest independent evolution, especially in the case of S.vulgaris (cf. Farner et al., 1982).

The failure of Z.l.gambelii to become photorefractory under 12L 12D is emphasized by the logarithmic growth constant, $k$, of group ETR after transfer to 20L 4D - 0.09 days$^{-1}$ - which is comparable to that of photosensitive males transferred directly from short to long days (Farner, Wilson, 1957). Therefore, as predicted by the second hypothesis, 12L 12D appear to induce none of the autumnal functions - photorefractoriness, postnuptial molt, and late-summer fattening. However, these results do not preclude the possibility that the process can begin on 12L 12D but requires longer days for its culmination.

The prediction that males in all groups will begin molt after the same number of days following transfer to long days, was also confirmed since the onset and duration of molt were virtually identical in all four groups. Thus, transfer of birds to long days appears to initiate the process that eventually induces the autumnal functions. The time required for induction of autumnal functions is independent of the stage of testicular development at the time of initiation of this delayed process. This strongly supports the hypothesis that autumnal and vernal functions are mutually independent.

However, it is useful to compare these results with those from birds transferred directly from short to long days. The duration of molt is identical in both cases, which is consistent with an additional hypothesis that the rate of autumnal functions is a direct function of the daylength at the time of their occurrence, which is generally consistent with the results of experiments on the postnuptial molt in F.coelebs (Gavrilov, Dolnik, 1974; Noskov, 1975, 1977). However, postnuptial molt began about 10 days earlier in all four groups transferred from 12L 12D relative to birds transferred directly from short days, indicating that this advance was independent of the duration of pretreatment with 12L 12D. This suggests that the process that induces the autumnal functions can begin on 12L 12D but requires longer days for its culmination.

We also obtained data in this experiment on the environmental control of premigratory fattening. Both prenuptial molt and vernal premigratory fattening are induced by 12L 12D. The intensity of prenuptial molt of the body feathers when plotted as a function of the duration of treatment with 12L 12D indicates that an apparently normal prenuptial molt is initiated and complet-

948

ed on 12L 12D. Premigratory fattening is also initiated but apparently persists indefinitely, even in those birds held on 12L 12D for over 400 days. However, when these birds were transferred to long days, premigratory hyperphagia apparently ceased and body weights decreased rapidly.

In Experiment II we (Moore et al., 1982) essentially reversed the manipulation of the photoperiodic regimen of Experiment 1. We employed 21 adult males captured in December at the same locality as those used in Experiment I. On 1 February these birds were transferred to constant-condition chambers with a photoregimen of 8L 13D after which on 5 March it was changed to 20L 4D. Thereafter one group was transferred to 12L 12D after 31 days, i.e., before testicular regression had begun. Testicular regression in this group was similar to that of controls on 20L 4D, but perhaps with a somewhat earlier onset and somewhat lower rate. None, however, underwent a postnuptial molt. Furthermore, in all members of a subset of this group returned to 20L 4D on day 70 testicular growth occurred, indicating that they were not photorefractory. This is consistent with the hypothesis that late summer set of functions can be induced only as a cluster and in an all-or-none manner.

The second group in Experiment II was transferred to 12L 12D after 60 days on 20L 4D, after the onset of photorefractoriness and testicular regression. In contrast with those transferred to 12L 12D after 31 days on 20L 4D, all of these birds molted and failed to undergo testicular growth. Therefore, molt can occur on a nonstimulatory photoregimen if photorefractoriness is first induced on longer days, which supports the hypothesis that these two functions are coupled. This is consistent with the results of experiments on F.coelebs by Noskov (1977).

The results of Experiment II indicate that the transfer from 20L 4D did not interrupt the sequence of late-summer events. Although further experiments are necessary, these results appear to be consistent with the conclusion of Dolnik (1975b), from experiments with F.coelebs, that photorefractoriness begins at a constant time after the end of the "unifactoral phase", i.e., logarithmic phase of testicular growth, even though there is as yet to physiologic rationale therefor.

Data on body weight from Experiment II are consistent with those from Experiment I, as well as with the hypotheses stated earlier in this communication. The weights of the birds transferred to 12L 12D after 31 days of 20L 4D were nearly maximal. Among those birds maintained on 12L 12D body weight remained elevated, whereas among those returned to 20L 4D after 39 days of 12L 12D weights decreased sharply in a manner similar to those in Experiment I. Body weights of control birds retained on 20L 4D and of the group transferred to 12L 12D on day 60 both decreased conspicuously. The latter underwent a very rapid postnuptial molt followed promptly by fattening. The control birds on 20L 4D also molted and fattened, but more slowly. Thus all of the late-summer functions proceeded more rapidly on 12L 12D, which supports the hypothesis that the rate of the late-summer functions is an inverse function of daylength at the time of their occurrence, and which is consistent with results reported for first-year and adult F.coelebs (Dolnik, Gavrilov, 1972; Gavrilov, Dolnik, 1974; Dolnik, 1976, 1980b; Noskov, 1975, 1977). The results of Experiments I and II both support the hypotheses proposed in the
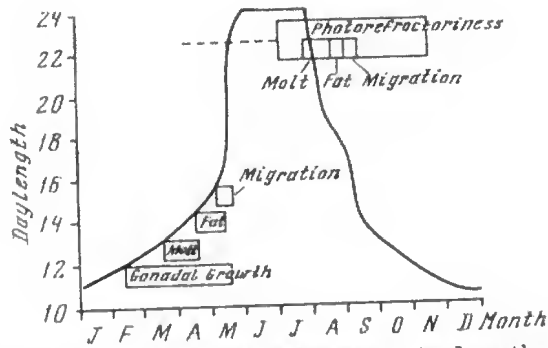
F i g. 2. The solid line depicts the changes in daylength experienced by a typical individual Z.l.gambelii throughout the year; note especially the rapid changes in daylength produced by latitudinal migration. The boxes depict the relative timing of the vernal and late-summer functions of the annual cycle and are drawn to suggest their relative independence of each other. The dotted line represents the slowly developing process that is induced by the vernal increase in daylength and that eventually causes the late-summer functions


Introduction and suggest strongly that essentially separate photoperiodic systems control the vernal and late-summer functions.

General observations of Z.l.gambelii under natural conditions (e.g. King, Mewaldt, 1981; Mewaldt, King, 1978; Morton, King, Farner, 1969; Wingfield, Farner, 1978) lend support to the conclusion that mechanisms that control the premigratory preparation in late summer differ from those of spring. Vernal premigratory preparation is highly synchronous within a given population, probably because it is induced directly by increasing daylength. In contrast, the preparation in late summer is much less synchronous, probably for two reasons: (1) Because daylengths are very long and change little at this time, no source of selectively predictive photoperiodic information, comparable to that of spring, is available. (2) Renesting can cause autumnal functions to be delayed in many pairs (Wingfield, Farner, 1979). Therefore, it seems likely that reliance on both a slowly developing or delayed process and internal coupling of functions in late summer evolved because (1) little usable external information is directly available and (2) renesting is adaptively more important than early, synchronous onset of preparation for migration.

Our current concept of the photoperiodic control of the annual cycle of Z.l.gambelii is depicted in Figure 2. As daylength increases in spring, it induces successively the independently controlled vernal functions - gonadal growth, molt, fattening, and migration. At least in part, these functions occur in proper sequence because each successive function has a slightly greater photoperiodic threshold. When the photoperiodic and local climatic conditions are suitable, northward migration begins. Our data suggest the intriguing hypothesis that the rapid increase in day length experienced during northward migration has an important function in the termination of fattening. There is also suggestive evidence that a similar response occurs during autumn when days shorten rapidly during southward migration. In any event.

this increase in daylength during vernal migration also initiates a delayed or slowly developing process that eventually induces late-summer functions. It is interesting that the entire reproductive effort occurs while this process is developing slowly. If the reproductive effort is extended due to re-nesting, the late-summer functions are further delayed. We have extensive evidence that this delay is produced by an inhibitory effect of high levels of sex steroid hormones (Matt, 1982; Wingfield, Farner, 1978), although the mechanism of maintenance of these high levels is unknown. In any event, the late-summer functions are induced as a coupled functional unit. Then, probably in response to a final component of the functional unit, southward migration begins. Once on the wintering grounds, short days terminate photorefractori-ness. It is then possible to begin another cycle once daylength increases in spring.

It will be obvious to those familiar with this subject, that this model is a specific example of the general "driver" hypothesis (Farner, Gwinner, 1980) in which the natural photocycle directly induces several independent components of the annual cycle. We include in this refined model for Z.l. gambelii (Fig. 2) the remote or delayed effects of long days and the internal coupling that effects the late summer-functions in their appropriate sequence. We have proposed herein that the components of the photoperiodic system of this taxon have evolved in response to very specific environmental const-raints. Therefore, we expect that these mechanisms will vary greatly among species in different environments and with different evolutionary histories. Indeed, in light of these considerations, it is not surprising that other species appear to rely on entirely different mechanisms, such as entrained endogenous circannual oscillators (cf. Berthold, 1974, 1979; Farner, Gwinner, 1981; Gwinner, 1981).

SUMMARY

Previous observations suggested that the photoperiodic mechanisms that control the preparation for vernal and autumnal migration are very diffe-rent. Results of two laboratory experiments on Zonotrichia leucophrys gambe-lii are consistent with this generalization, indicating (1) that the vernal functions are relatively independent events that are induced directly by changes in daylength, but (2) that autumnal functions are induced as an in-ternally coupled cluster by a slowly developing process that is induced by vernal increases in daylength. The time of onset of the latter is an in-verse function of daylength, but after onset the time required to complete the functions is a direct function of daylength.

R e f e r e n c e s

Berthold P. - Endogene Jahresperiodik. Konstanz: Universitätsverlag, 1974.
Berthold P. - Vogelwarte, 1979, 30, p. 7-10.
Dolnik V.R. - Migratsionnoe Sostoyanie Ptits. Moskva: Nauka, 1975a.
Dolnik V.R. - Zool. Zhur., 1975a, 54, p. 1048-1056.
Dolnik V.R. - In: Fotoperiodizm Zhivotnik i Rastenii / Ed. by V.A.Zaslavskii. Leningrad: AN SSSR, 1976, p. 47-81.

Dolnik V.R. - In: Problemy Kosmicheskoi Biologii. V. 41 / Ed. by V.N.Cher-
    nigovskii.  Biologicheskii Ritmy. Moskva: Nauka, 1980, p. 238-288.
Dolnik V.R. - Zool. Zh.,1980b, 59, p. 91-98.
Dolnik V.R., Gavrilov V.M. - Zool. Zhur., 1972, 51, p. 1685-1696.
Farner D.S. - Amer. Sci., 1964, 52, p. 137-156.
Farner D.S. - Environ. Res., 1970, 3, p. 119-131.
Farner D.S., Donham R.S., Matt K.S. et al. - In: Avian Endocrinology: En-
    vironmental and Ecological Perspectives / Eds. S.Mikami et al. Tokyo:
    Japan Science Societies Press, 1982.
Farner D.S., Donham R.S., Moore M.C. - Physiol. Zool., 1981, 54, p. 372-378.
Farner D.S., Donham R.S., Moore M.C. - Auk, 1980, 97, p. 63-75.
Farner D.S., Follett B.K. - In: Hormones and Evolution. Vol. 2 / Ed. by
    B.J.Barrington. L.: Academic Press, 1979, p. 829-872.
Farner D.S., Gwinner E. - In: Avian Endocrinology / Eds. A.Epple, M.H.Stet-
    son. N.Y.: Academic Press, 1980, p. 331-336.
Farner D.S., Lewis R.A. - Photophysiology, 1971, 6, p. 325-370.
Farner D.S., Wilson A.C. - Biol. Bull.., 1957, 113, p. 259-267.
Gavrilov V.M., Dolnik V.R. - Tr. Zool. Inst., 1974, 55, p. 14-61.
Gwinner E. - In: Handbook of Behavioral Neurobiology 4. Biological Rhythms /
    Ed. by Aschoff. N.Y.: Plenum, 1981, p. 391-410.
Gwinner E., Dittami J., Gänshirt G. - Vogelwarte, 1980, 30, p. 335-337.
King J.R. - Condor, 1961, 63, p. 128-142.
King J.R., Farner D.S. - Condor, 1963, 65, p. 200-223.
King J.R., Mewaldt L.R. - Auk, 1982, 98, p. 752-764.
Matt K.S. Doctoral dissertation, University of Washington, Seattle, 1982.
Mattocks P.W. Jr. Doctoral dissertation, University of Washington, Seattle,
    1982.
Mattocks P.W. Jr., Farner D.S., Follett B.K. - Gen. Comp. Endocrinol., 1976,
    30, p. 156-161.
Mewaldt L.R., King J.R. - North Amer. Bird Bander, 1978, 3, p. 138-144.
Morton M.L., King J.R., Farner D.S. - Condor, 1969, 71, p. 376-385.
Murton R.K.,Westwood N.J. Avian Breeding Cycles. Oxford: Clarendon Press,
    1977.
Noskov G.A. - Zool. Zhur., 1975, 54, p. 413-424.
Noskov G.A. - Zool. Zhur., 1977, 61, p. 1676-1686.
Stresemann E., Stresemann V. - J. Ornithol. (Sonderheft), 1966, 107, p.1-447.
Wingfield J.C., Farner D.S. - Biol. Reprod., 1978, 19, p. 1046-1056.
Wingfield J.C., Farner D.S. - Gen. Comp. Endocrinol., 1979, 38, p. 322-331.
Wingfield J.C., Farner. - Prog. Reprod. Biol., 1980, 5, p. 62-101.

# THE ROLE OF THE HYPOTHALAMO-HYPOPHYSIAL SYSTEM IN THE ANNUAL CYCLE OF MOLT AND GONADAL FUNCTION

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The seasonal cyclic character of reproductive function and of its closely related morphogenic processes is effected through an interaction of endogenous and exogenous factors. Among the internal factors the hypothalamo-hypophysial system plays the leading role. It possesses a high degree of functional plasticity that ensures a broad spectrum of adaptations of seasonal morphogenic processes to external environmental conditions.

Various authors have demonstrated that the surgical blockade of the transport of gonadotrophin-releasing hormone(s) to adenohypophysis causes gonadal regression. Sexual maturation and seasonal activation of avian gonads is related to an increase in secretory function of the preoptic-supraoptic region and of the infundibular nuclear complex. Our own studies have demonstrated that electrolytic lesions in the afore-mentioned hypothalamic regions cause a depression of pituitary gonadotropic function in ducks.

Gonadoliberin-synthesizing neurons (LH-RH) in birds have been demonstrated mostly in the preoptic region (Bons et al., 1978). The infundibular complex contains a much smaller quantity of these neurons. The axons of LH-RH-producing neurons from these hypothalamic regions project into the external layer of the median eminence where they contact the capillaries of the portal vessels. According to Davis (1980) the supraoptic region may serve as a positive steroid feedback center and may also be involved in the retino-hypothalamic system. Using light-conducting fibres it has been demonstrated that photosensitive receptors are localized mainly in the ventromedial hypothalamus (Yokoyama et al., 1978).

The secretion of gonadotrophins in male birds, as in mammals, is tonic, whereas it is cyclic in females. The maximum level of LH in the blood of hens occurs 4-6 hours before the ovulation (while in cockerels the daily level of LH does not change significantly). Sexual dimorphism is also reflected in the blood level of FSH. As in mammals the sexual differentiation of the hypothalamus is determined by androgens. However a problem arises with respect to the nature of this phenomenon in birds with their different genetic determination of sex. We solved this problem using the procedure of cross-transplantation of gonads in castrated male and female of the Pekin ducklings. It was found that in the reproductive period in males with transplanted ovaries a cyclic type of LH secretion is established. In castrated females with transplanted testes LH secretion becomes tonic. These findings suggest that in birds the sexual differentiation of hypothalamus is manifested clearly in the reproductive period and is determined by estrogens.

In male Pekin ducks the blood level of FSH is five times higher than in females. Following castration of males with transplanted ovaries the FSH content of the blood is reduced to the level observed in females. The mass of the testes relative to the total body mass in the Pekin duck is 9% while in geese it is only 6.25%. The level of plasma FSH is 450% higher in male ducks than in females, but only 30% higher in male than in female geese. The ex-

traordinarily high blood levels of FSH in male ducks is apparently related
to the development of the large testicular mass during the period of maximal
sexual activity. Species and strain differences of relative testicular mass
are determined by genetically fixed differences in secretion of gonadoliberin
by the hypothalamus. This conclusion is based on the results of our experi-
ments with cross-transplantation of two testes of bantham chicks and those
of white leghorns, as well as between Pekin and wild ducks. In the reproduc-
tive period the transplanted gonads always attained the mass characteristic
of the recepient.

It is well-known that the function of the reproductive system in birds is
closely related to the annual cycle of daylength. A characteristic feature
of photosensitive birds is that their gonads after the active period, return
to a resting state. This phenomenon is related to the temporary loss of the
photosensitivity of the control system. There are considerable species diffe-
rences in the duration of the photorefractory period. The shift of the rep-
roductive system into the photorefractory phase may be related with a seaso-
nal feature of hypothalamic secretion of LH-RH. We made experiments with si-
mulation incubation, in the body cavity of photorefractory house sparrows,
of the inactive testes with the adenohypophyses and hypothalami of birds in
various stages of the photo-induced sexual cycle. It was found that activat-
ion of the spermatogenic epithelium occurred in only those cases in which
the hypothalamus was taken from birds in the early phase of the sexual cycle.
It has also been demonstrated that the injections of synthetic LH-RH led to
an increase in secretion of gonadotropins in photorefractory _Zonotrichia_
(Wingfield et al., 1979), and in ducks (Bogach et al., 1980). The increase
of the level of LH in males is accompanied by a considerable increase in
testosterone concentration in the blood. These findings suggest that in the
refractory period the level of LH-RH in the hypothalamus is decreased. Howe-
ver, these experiments do not answer the question whether the mechanisms of
photorefractoriness are restricted to hypothalamic level. At that stage the
hypothalamus probably loses its ability to secrete into portal circulation
a sufficient quantity of LH-RH, or some extra-hypothalamic regulators are
eliminated.

Biogenic amines are involved in the regulation of function of the hypo-
thalamo-hypophysiogonadal system. Various authors have demonstrated positive
correlations between concentration of catecholamines in the hypothalamus and
concentration of gonadotropins in blood. It has been shown that the deplet-
ion of the monoamine (MA) depots in the brain by reserpine injections causes
regression of the gonads in the pigeon, and prevents the gonadal response to
the light in ducks (see Tienhoven, 1981). In our studios with ducks it was
noted that the implantation of serotonin into the third ventricle of the
brain results in a decrease of the LH level in blood plasma both in young
photosensitive ducks and adult males in the reproductive phase (Rudneva et
al., 1978). Adrenomimetic drugs given intraventricularly increase the con-
centration of gonadotropins in the blood in these birds (Novikov, Rudneva,
1981). These results indicate that monoamines participate in the regulation
of release of gonadotropins and are a necessary component of the hypothalamo-
hypophysial regulation of gonadal function. However, the mechanisms of action

of monoamines are still incompletely understood. It is assumed that they are active in the process of transfer of releasing hormones from the median eminence to the adenohypophysial portal vessels (Weiner, Ganong, 1978).

The hypothalamic control of the gonadal function is effected mainly on the basis of feedback mechanisms. Our studies have demonstrated that the implantation of testosterone or estradiol into the III ventricle or infundibular region of ducks depresses gonadotropin secretion. However in castrated birds, significant changes in the seasonal cyclicity of gonadotropin secretion do not occur (Novikov, Felix, 1972; Mattocks et al.,1976). These results are difficult to interpret on the basis of feedback principle.

The neuroendocrine system controls the second periodic morphogenic process - molting. The autumn molt occurs after the cessation of the reproductive season as a result of an alteration of the balance of hormonal factors in the organism. The molt and reproductive cycles are dissociated in phase. Considerable species differences occur in the characteristics of phase relationships of these processes.

It is known that the molting is preceded by intense proliferation of cells of the deep epidermal layers of the feather follicle and by increased growth of the papilla of the feather. As a result the adhesion of the feather tip to the walls of its follicle weakens. This process is controlled by thyroxin and somatotropic hormone, which stimulate the proliferation of epidermal cells at the expense of an acceleration of the S-period of the cell cycle. The change of feather is related to a marked increase in plasma levels of thyroxin, corticosterone and somatotropic hormone. The hypothalamus plays the leading role in the system of endogenous regulatory mechanisms of molting and feather development. It was demonstrated in our studies with ducklings that electrolytic lesions of the ventromedial nucleus region results in a delay of the feather development and of total growth of feathers. These processes are accompanied by depression of thyrotropic and somatotropic functions of the adenohypophysis.

In our studies on _Lagopus lagopus_ the special regional characteristics of molting were found to depend on differential sensitivity of feather-forming tissues to hormones. It is characteristic that castration of birds with a prolonged sexual cycle (hens, ducks) results in a permanent change in plumage.

The cyclic periodicity of the molting processes is related to photoperiodicity. Photostimulation in an unusual time of the year results in a shifting of reproductive and molt periods. Following the transfer of birds from long to short photoperiod the molting process is accelerated. These observations suggest that alternating temporal pattern of reproductive and molting cycles is controlled by interdependent functions of the neurohormonal mechanisms of their regulation. The conditions of light-dark regime in these processes play mostly a role of a triggering factor.

The hypothesis of an integrated function of the neuroendocrine system in the control of reproduction and molt is supported convincingly by evidence obtained in studies on neuroendocrine mechanisms of the stress-induced molting of hens that is used in poultry-farming. The forced molting is induced by abrupt change in the light regime, feeding conditions and water-salt metabolism. According to our observations, these stressors lead to a profound

depression of the neurohormonal system that regulates reproductive function and activation of hormonal function of the thyroid complex, of the adrenal cortex, and of adenohypophysial somatotropocytes. In contrast, following normalization of living conditions and increase of photoperiod, the reproductive control system is activated while the function of the neuroendocrine complex of molting control is depressed. The findings of this report demonstrate that the periodic alterations in time of truly reproductive and molt cycles is related to an integrated annual cyclic periodicity in the function of neurohormonal mechanisms.

R e f e r e n c e s

Bons N., Kerdelhue B., Assenmacher J. - Cell Tissue Res., 1978, 188, p.99-106.
Bogach P.G., Novikov B.G., Rudneva L.M., Bajev V.V. - Dokl. AN USSR. Ser. B, 1980, N 9, p. 63-66.
Davies D.T. - Proc. R. Soc. Lond., 1980, B 206, p. 421-437.
Mattocks P.W., Farner D.S., Follett B.K. - Gen. Comp. Endocrinol., 1976, 30, p. 156-161.
Novikov B.G., Felix L.S. - Probl. phiziol. hypothal (Kiev), 1972, 6, p. 127-132.
Novikov B.G., Rudneva L.M. - Fiziol Zhur., 1981, 27, p. 117-120.
Rudneva L.M., Novikov B.G., Dzerjinsky N. - Dokl. AN USSR, 1978, N 2,p.82-84.
Tienhoven A. Van. - World Poult, Sci. J., 1981, 37, p. 156-176.
Weiner R., Ganong W. - Physiol. Rev., 1978, 58, p. 905-976.
Wingfield J.C., Crim J.W., Mattocks P.W., Farner D.S. - Biol. Reprod., 1979, 21, p. 801-806.
Yokoyama K., Oksche A., Darden T., Farner D.S. - Cell Tissue Res., 1978, 189, p. 441-450.

# ANATOMY AND PHYSIOLOGY OF THE AVIAN RESPIRATORY SYSTEM

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## INTRODUCTION

This brief review is meant to provide the anatomic and physiologic basis
for a better understanding of the remaining contributions in this Symposium.
Thers has been a considerable progress over the last decade in avian respi-
ratory physiology and a number of reviews have been devoted to the subject
(quoted in Scheid, 1979, 1982).

## ANATOMY OF THE RESPIRATORY SYSTEM

Gross and microscopic anatomy of the avian respiratory system has been
investigatsd for a great numbsr of bird species in recent years (cf. Dun-
cker, 1971, 1972). Whereas interesting species differences have been obser-
ved in certain structural aspects, the uniformity of the respiratory system
is particularly striking and enables the physiologist to depict simplified
schemes which can bs used for a functional analysis of the rsspiratory sys-
tem in birds in general.

Figure 1 shows the elements of the avian respiratory tract. In the la-
teral view, the lung appears as a relatively small organ in the dorsal part
of the thoracoabdominal cavity. The lung is surrounded by large air sacs
(Fig. 1 A, B).

Plastic casts havs revealed the architecture of the lungair sac apparatus.
Compared with the mammalian bronchial tree, there exist only few bronchial
generations in birds (Fig. 1 B). Two main bronchi originate from ths trachea
which entsr each lung at its cranio-ventral side. The main bronchus givss
rise to two sets of secondary bronchi, the medioventral and the mediodorsal
secondary bronchi, which are connectsd by the long, narrow tertiary bronchi,
the parabronchi.

Two groups of air sacs may be discerned according to their bronchial con-
nection (Fig. 1 B). The cranial group (cervical /not shown in Fig. 1/, cla-
vicular and cranial thoracic air sacs) originate from the medioventral se-
condary bronchi, while the caudal group (caudal thoracic and abdominal air
sacs) connsct to the main bronchus.

The parabronchial walls are formed by blood capillariss and air capil-
laries (Fig. 1 C). Blood capillaries conduct blood from the periphery of the
periparabronchial tissue to collecting venules at the luminal wall. Air ca-
pillaries form a meshwork which intermingles with the blood capillaries,pro-
viding a large area for respiratory gas exchange.

## VENTILATORY FLOW IN THE RESPIRATORY TRACT

By the action of inspiratory muscles the air sacs are expanded on in-
spiration and air enters the respiratory tract via the trachea. On its pas-
sage into ths air sacs, part of the inspired air crosses the parabronchi
of the lung to exchange $O_2$ and $CO_2$ with the blood. Comprsssion of the air
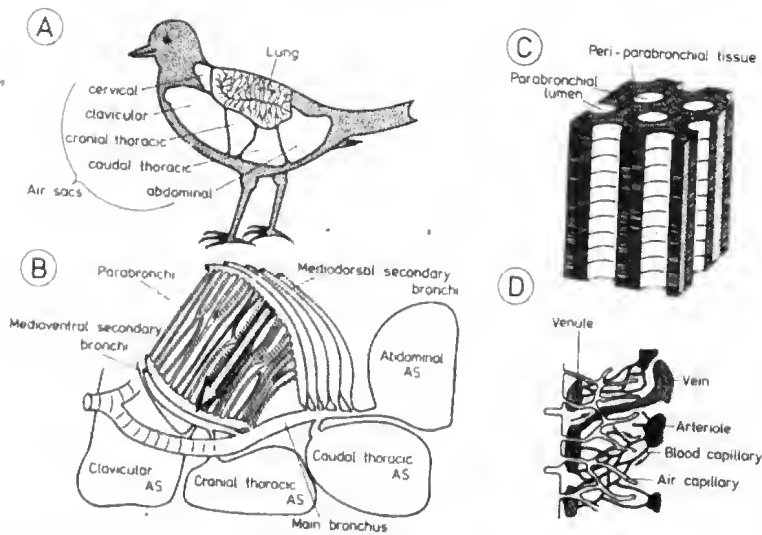
F i g. 1. Schematic representation of the lung-air sac system in birds. AS, air sac. For details, see text

sacs during expiration creates expiratory flow, part of which ventilates the parabronchial lung.

Direct measurement in the mediodorsal secondary bronchi has shown that flow through the parabronchi is unidirectional, i.e. assumes the same direction in both respiratory phases; from the mediodorsal to the medioventral end (arrow in Fig. 1 B).

Recently, Powell et al. (1981) have used a mass spectrometer to measure partial pressures of $O_2$ ($P_{O_2}$) and $CO_2$ ($P_{CO_2}$) at various positions in the bronchial system of spontaneously breathing ducks. These respiratory gas profiles revealed a close to complete functional valving of ventilatory gas flow (Fig. 2). During inspiration, part of the air enters the caudal air sacs directly, the other part passes through the parabronchial lung to enter the cranial air sacs which do not receive any inspired air directly through the medioventral secondary bronchi. During expiration, most, if not all, gas leaving the caudal air sacs passes through the parabronchi, there being virtually no gas exiting directly through the main bronchus, while cranial air sac gas leaves directly via the medioventral secondary bronchi.

The exact mechanism for this functional valving is unknown. There is no evidence for anatomical valves; aerodynamic valving appears to play a significant role. The functional significance of unidirectional flow, in particular its importance for gas exchange will be considered below.

GAS EXCHANGE IN THE PARABRONCHUS

The essential structural elements of the parabronchus in respect of gas exchange are the following (see Fig. 3):

1. The parabronchus constitutes a long tube that is open at both ends and thus allows continuous air flow from one to the other end.

2. Blind-ending air capillaries originate from the parabronchial lumen to pass in radial direction into the periparabronchial tissue. Gas exchange along the air capillaries is by diffusion.
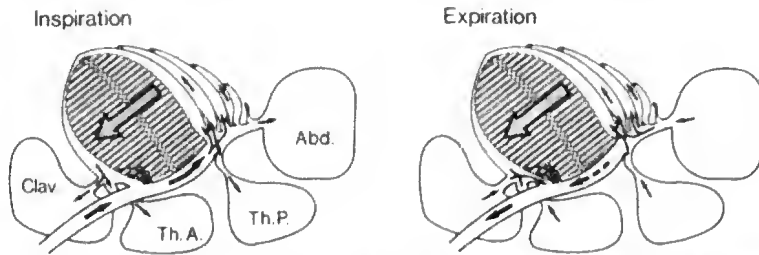
F i g. 2. Direction of air flow in the bronchial system during inspiration (left) and expiration (right). The dashed arrow of expiratory flow in the main bronchus corresponds to an unknown, but probably small fraction of expiratory flow exiting caudal air sacs directly via main bronchus. Abbreviation for air sacs: Clav., clavicular; Th. A., cranial thoracic; Th. P., caudal thoracic: Abd., abdominal
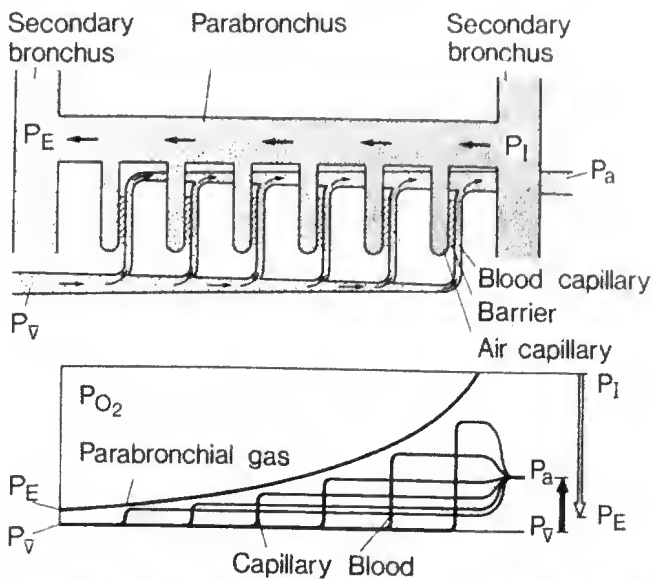


F i g. 3. Schema of serial-multicapillary or cross-current system for gas exchange in the avian parabronchus. $P_{O_2}$ in gas entering ($P_I$) and leaving ($P_E$) parabronchus, and in mixed arterial ($P_a$) and mixed venous blood ($P_{\bar{V}}$). For details, see text

3. Blood capillaries contact the air capillaries all along the parabronchus.

4. A thin tissue membrane separates air capillaries and blood capillaries. Diffusion constitutes the mechanism of gas transfer across this membrane.

Consider a volume of air entering the parabronchial lumen from the mediodorsal secondary bronchus. Oxygen in this air enters blood of the first blood capillary. Thereby, the $P_{O_2}$ in the gas volume drops as it passes down the parabronchial lumen to the site of origin of the next capillary (Fig. 3, lower diagram). This results in a continuous decline of $P_{O_2}$ in the air along the parabronchus. Likewise, blood perfusing the capillaries differs in the degree of arterialisation, there being a drop from the gas entrance end to the outflow end of the parabronchus. Gas leaving the parabronchus contains

the lowest $P_{O_2}$ ($P_E$), while arterial blood, resulting as a mixture from all capillaries, may well be higher in $P_{O_2}$ than $P_E$.

This is depicted in the lower part of Fig. 3 where the $P_{O_2}$ profiles in parabronchial gas and in capillary blood are shown. The crossing-over of partial pressures in the gas and (mixed) blood phases, which is particularly prominent for $CO_2$, reflects the efficient performance of this serial-multi-capillary or cross-current system, the efficacy of which is higher than that of the ventilated pool system of mammalian alveolar lungs (Piiper, Scheid, 1975).

## SIGNIFICANCE OF UNIDIRECTIONAL FLOW

It is apparent from Fig. 3 that reversal of the flow direction in the parabronchus does not affect the overall gas exchange, there being merely a reversal in the sequential order of blood capillaries which, however, does not affect the composition of mixed arterial blood. The question has, therefore, been raised as to the physiological significance of the fact that parabronchial flow is unidirectional under normal breathing conditions.

An important factor may be the avoidance of zero flow that would result from flow reversal. Since the gas volume contained in the parabronchial lumina is small (as compared to mammalian alveolar space), a rapid drop of $P_{O_2}$ and a rapid rise of $F_{CO_2}$ are expected when parabronchial flow drops to zero.

Furthermore, the reversal of flow may necessitate additional energy expenditure for acceleration and deceleration of air flow. Micro-anemometric measurements in dorsobronchi have revealed air flow in dorsobronchi to be remarkably smooth during breathing at elevated frequencies (panting).

In most birds there exists an additional system of parabronchi which mainly connects the main bronchus and dorsobronchi to the caudal air sacs. This system, termed "neopulmo" by Duncker (1971), is particularly well developed in song-birds. In these birds, the main bronchus, caudal to the origins of dorsobronchi, is very much reduced so that the abdominal air sacs are connected to the dorsobronchi by neopulmonary parabronchi only. Therefore, air flow in these parabronchi must be in opposite directions during inspiration and expiration, respectively. Since their microscopic structure suggests that the cross-current system applies to neopulmonic parabronchi as well, it is evident that unidirectional air flow is not mandatory for parabronchial gas exchange.

## BIRDS VS. MAMMALS: ADVANTAGES OF THE AVIAN RESPIRATORY SYSTEM

The avian respiratory tract, with the differentiation of lungs proper and air sacs, with the complex air flow pattern and the cross-current system, is expected to offer some advantages over the mammalian lungs with their simpler construction. When comparing the avian with the mammalian respiratory system from the physiological point of view, the following advantageous features may be conjectured.

1) The gas exchange efficacy of a cross-current system is higher than that of the ventilated pool system considered to be the simplest adequate model for mammalian lungs. The higher efficiency may be essential for sustained flight, particularly at high altitude.

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2) The absence of larger volume changes of the lung during respiration may help to avoid problems arising from changes in radius of curvature and surface tension.

3) In birds, the fraction of total ventilation passing through parabronchi appears to be easily variable by changes of the extent of "shuot flow" serving to ventilate air sacs only. In air sacs, gas exchange is small to negligible, but heat exchange is probably extensive. Thus heat and gas exchange may be more easily dissociated from each other than in the mammalian respiratory tract.

### SUMMARY

The avian respiratory apparatus comprises two components: (1) The air sacs which act as bellows to provide tidal respiratory air flow during inspiration and expiration. (2) The parabronchial lung in which gas exchange occurs between air in the air capillaries and blood perfusing the blood capillaries. Ventilatory flow through the open-ended parabronchial tubes assumes the same direction both during inspiration and expiration. Gas exchange in the parabronchus can adequately be described by a cross-current model, the efficiency of which is superior to that of the alveolar lung. Although parabronchial gas exchange is independent of air flow direction, unidirectional air flow appears to be advantageous.

### R e f e r e n c e s

Duncker H.-R. - Ergebn. Anat. Entwckl.-Gesch., 1971, 45, N 6,

Duncker H.-R. - Respir. Physiol., 1972, 14, p. 44-63.

Piiper J., Scheid P. - Respir. Physiol., 1975, 23, p. 209-221.

Powell F.L. et al. - Respir. Physiol., 1981, 44, p. 195-213.

Scheid P. - Rev. Physiol. Biochem. Pharmacol., 1979, 86, p. 138-186.

Scheid P. - In: Avian Biology. Vol. VI / Eds. D.S.Farner, J.R.King. Academic Press, 1982.

# INERT GAS TRANSFER AND FUNCTIONAL INHOMOGENEITIES IN AVIAN LUNGS

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The evolution of the respiratory system of terrestrial vertebrates is characterized by an increase in gas exchange surface area. This was necessary to allow the increased oxygen uptake required by endothermy and more energetic forms of locomotion (assuming a fixed composition and minimal thickness of the blood gas barrier and a maximum oxygen tension driving the diffusive process). The increased surface area was achieved by partitioning the lung into many finer subunits resulting in a larger surface: volume ratio. The emergence of this strategy is nicely shown within the reptiles. Varanid lizards which are very active predators with high aerobic scopes have a multicameral lung with many more subdivisions than the paucicameral lung of Iguanid lizards which have a more limited aerobic scope (Mitchell et al., 1981; Perry, Duncker, 1978).

At some point in the early evolution of the reptiles, the way in which lungs were partitioned diverged. The end results of this divergence are the mammals with homogeneous partitioning and the birds with heterogeneous partitioning (Duncker, 1978). Although structural differences between avian and mammalian lungs may lead to differences in the efficacy of gas exchange (cf. Scheid, this volume), one common factor which can reduce the efficacy of gas exchange in either type of lung is functional inhomogeneity. That is, ventilation and blood flow (perfusion) may not be optimally matched with one another, or with the diffusive properties in the individual subdivisions of a highly partitioned lung. This reduced efficacy is one of the "costs" of increasing surface area by partitioning and it is reasonable to ask the question, "Is this reduced efficacy of gas exchange from functional inhomogeneities (i.e. "partitioning cost") more or less in avian lungs compared to mammalian lungs?".

## INERT GAS TRANSFER

Inert gases are useful in studying the effects of ventilation-perfusion mismatching in lungs for several reasons. Firstly, inert gases are those gases which do not enter into chemical reactions with the blood (like $O_2$, CO and $CO_2$ do). Hence, one can study the gas exchange properties of the lungs independent of blood chemistry and not be confounded by differences in hemoglobins, for example. Secondly, because inert gases are only carried in physical solution by the blood they obey Henry's law and show linear blood-gas dissociation curves. This constant realtionship between blood contents and partial pressures allows one to write analytical descriptions of their transfer for various lung models. Thirdly, because inert gases come rapidly to diffusion equilibrium across the blood-gas barrier, they are virtually unaffected by diffusive/perfusive functional inhomogeneities (Piiper, Scheid, 1980). In fact, the efficacy of an inert gas' transfer in avian and mammalian lungs is primarily a function of ventilation/perfusion (V/Q) equality.
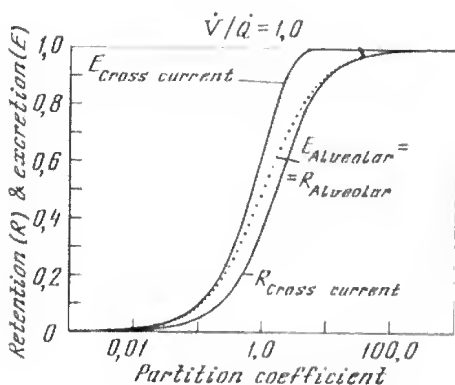
F i g. 1. Excretions and retentions of inert gases, not present in the inspirate, being eliminated from venous blood as a function of their blood-gas partition coefficient. For homogeneous alveolar lungs, E=R for all gases while $E \gtrsim R$ in cross-current lungs, indicating greater efficacy of cross-current gas exchange. A more familiar example of superior efficacy in cross-current compared to alveolar exchangers is $Pa_{O_2} > PE_{O_2}$ and $PE_{CO_2} > Pa_{CO_2}$ in birds while expired gas and arterial blood are in equilibrium in mammals

Consider first the elimination of an inert gas from venous blood in a single subunit of a mammalian lung (i.e. alveolus) or an avian lung (i.e. parabronchus). Gas exchange can be described in terms of excretions (E) and retentions (R) by normalizing expired and arterial to mixed venous partial pressures as:

$E = PE/P\bar{v}$ and $R = Pa/P\bar{v}$

Because elimination of a gas is directly proportional to E, or PE, for fixed $\dot{V}/\dot{Q}$ and $P\bar{v}$ (i.e. $\dot{M}_x \propto \dot{V}PE_x$), greater E for the same gas and ventilation in one compared with the other lung indicates greater efficacy. Similar arguments hold for R and $\dot{Q}$ (Farhi, Plewes, 1980). Figure 1 shows that the efficacy of the cross-current exchange (for the avian lung) is greater than alveolar. If birds do not eliminate inert gases better than mammals, then (a) $\dot{V}/\dot{Q}$ inequality may depress inert gas elimination more in avian lungs or (b) birds may have more $\dot{V}/\dot{Q}$ inequality.

The effects of $\dot{V}/\dot{Q}$ inequality on inert gas elimination were examined with a computer model of cross-current gas exchange first. Equations predicting expired gas and arterialized blood concentrations of inert gases were solved for 50 gas exchange units (representing parabronchi), each of which could have different values of ventilation, perfusion and $\dot{V}/\dot{Q}$. Thus, parallel $\dot{V}/\dot{Q}$ inequality between parabronchi was studied. Serial inequality of blood flow along a parabronchus will not affect inert gases (Powell, Wagner, 1982a) so blood flow was assumed to be uniformly distributed within a given exchange unit for simplicity. Ventilation and perfusion were distributed between the individual units as logarithmic normal distributions because (a) this method has been previously employed to study the effects of inhomogeneity in alveolar lungs (West, 1969), (b) many biological variables are described by log-normal distributions and (c) most importantly, the inhomogeneity can be described by a single parameter - the log-standard deviation of the distribution. Furthermore, a given log-standard deviation of either blood flow or ventilation distributions has an equal effect on depressing the efficacy of gas exchange. Computing flow weighted means of inert gas partial pressures in blood and gas leaving the individual exchange units gives whole lung retentions and excretions.
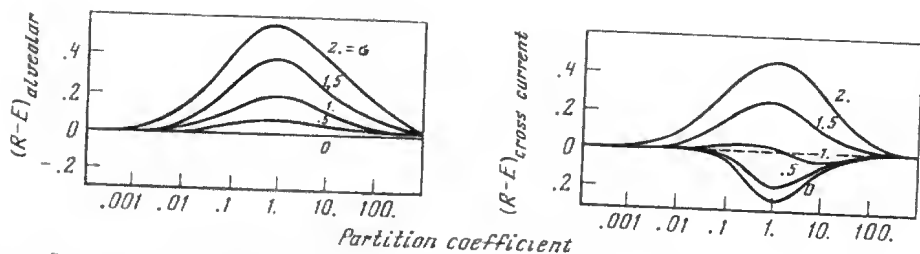
F i g. 2. Retention-excretion (R-E) difference for gases with different blood-gas partition coefficients in 50 compartment alveolar (upper) and cross-current (lower) gas exchangers with overall $\dot{V}/\dot{Q}=1$. As $\dot{V}/\dot{Q}$ inequality increased (R-E) increases indicating reduced efficacy. However, the difference is greater (or equal) with any amount of inequality in alveolar compared to cross-current exchangers. Partition coefficients between 0.1 and 10 are of the most physiologic interest because this range encompasses the various values associated with $O_2$ and $CO_2$ exchange

Figure 2 shows retention-excretion differences, which are proportional to arterial-expired differences (vide supra) for both alveolar and cross-current lungs with various amounts of $\dot{V}/\dot{Q}$ inequality. When the log-standard deviation (σ) of the distributions is zero, this difference is less in cross-current than in alveolar lungs for gases of any partition coefficient (as was the case in Figure 1). With increasing inequality (σ), gas exchange efficacy drops in both models as the retention-excretion difference becomes more positive. This is similar to a diffusion impairment reducing efficacy by increasing the arterial-expired gradient. However, note that for any degree of inequality the cross-current lung always performs better than the alveolar lung. Hence, $\dot{V}/\dot{Q}$ inequality should not depress inert gas elimination in bird lungs more than in mammalian lungs unless there is more of it.

MEASUREMENT OF $\dot{V}/\dot{Q}$ INEQUALITY IN BIRDS

To assess the mismatching of ventilation and blood flow among parabronchi, our laboratory has applied the multiple inert gas elimination technique to tidally ventilated geese (Powell, Wagner, 1982b). This technique is based on the fact that retentions and excretions of inert gases being eliminated from the blood are a function of their blood-gas partition coefficient and the $\dot{V}/\dot{Q}$ (vide supra). By simultaneously measuring retention and excretion of several inert gases with different partition coefficients, one can use statistical techniques to infer a $\dot{V}/\dot{Q}$ distribution (Powell, Wagner, 1982a; Wagner, West, 1980).

Figure 3 shows a typical $\dot{V}/\dot{Q}$ distribution measured in our geese. The notable features are (a) there is no blood flow shunt or low $\dot{V}/\dot{Q}$ areas; i.e. pulmonary blood flow is only perfusing well ventilated lung regions, (b) there is measurable dispersion of the $\dot{V}/\dot{Q}$ distribution around the overall value for the lung of 1.0; σ for the main $\dot{Q}$ distribution averaged 0.6, (c) about 10% of total ventilation (or 17% of non-deadspace ventilation) was to poorly perfused lung regions. Contrasting this distribution to a mammal's under comparable conditions, the mammal (a) also has no appreciable shunt or low $\dot{V}/\dot{Q}$,
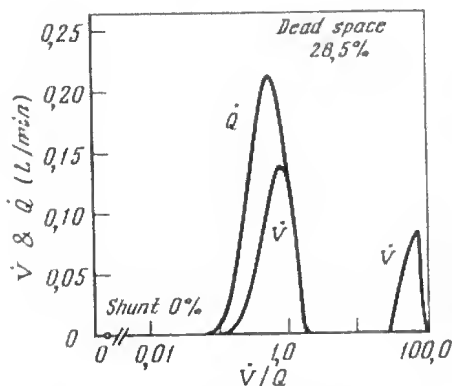
F i g. 3. Ventilation ($\dot{V}$) and blood flow ($\dot{Q}$) as a function of ($\dot{V}/\dot{Q}$) in different cross-current gas exchange units of geese (after Powell and Wagner, 1982b)

(b) has a main $\dot{Q}$ mode which is narrower ($6 \approx .35$), and (c) usually has no high V mode. However, after correcting for dead-space, the measured retention-excretion differences were negative in birds but positive in mammals ( Powell, Wagner, 1982 a, b; West, Wagner, 1977 ). Hence, even though the geese had more measurable $\dot{V}/\dot{Q}$ inequality, their efficacy of inert gas elimination was better than would be possible with alveolar lungs.

EFFECTS OF $\dot{V}/\dot{Q}$ INEQUALITY ON $O_2$ AND $CO_2$ EXCHANGE

Although inert gases are useful tools for studying functional inhomogeneities, oxygen and carbon dioxide are the gases of physiological significance. The effect of $\dot{V}/\dot{Q}$ inequality on $O_2$ and $CO_2$ exchange have been modeled for alveolar lungs using an approach similar to that described above for inert gases (West, 1969). The only difference is that computer algorithms for the nonlinear dissociation curves of $O_2$ and $CO_2$ in blood (Kelman, 1966, 1967) are necessary to relate contents and partial pressure instead of the physical solubility as used for inert gases. Bohr-Haldane effects are taken into account and diffusion equilibrium is assumed as it was for inert gases. The effects of $\dot{V}/\dot{Q}$ inequality in cross-current lungs can be modeled similarly. If the same algorithms for $O_2$ and $CO_2$ dissociation curves are used in alveolar and cross-current models then one can again compare the efficacy of the two lung types with varying degrees of inhomogeneity, given a certain blood chemistry. (However, notice that such modeling could also be used to investigate the consequences of avian-mammalian differences in blood chemistry by substituting different algorithms.)

The effects of an acutely creating $\dot{V}/\dot{Q}$ inequality in alveolar or cross-current lungs is similar - both models would decrease $O_2$ uptake and $CO_2$ elimination. $O_2$ uptake is generally depressed more than $CO_2$ output ( $\approx$ 82% of homogeneous value for $O_2$ vs. $\approx$ 87% for $CO_2$ in both models with $\sigma$ = 1). This has been shown to be a function of differences in $O_2$ and $CO_2$ dissociation curves in mammals (West, 1969/70) and is presumably the case in birds also. Although this exercise is interesting, it is not very physiological. In real life $O_2$ consumption is maintained when challenged by inhomogeneities through readjustment of blood gases.

Figure 4 shows the effects of $\dot{V}/\dot{Q}$ inequality on blood-gases when $O_2$ uptake and $CO_2$ output are maintained at normal resting levels. For $CO_2$, the arterial-expired, or arterial-alveolar, differences are analogous to the retention-excretion differences with inert gas elimination discussed above. In the homogeneous case ($\sigma$ = 0) this difference is negative for cross-current lungs and zero for alveolar lungs, similar to inert gases. With increasing

Fig. 4. Blood (arterial)-gas(expired or alveolar) differences for $O_2$ and $CO_2$ in alveolar (dashed line) and cross-current lungs (solid line) with increased $\dot{V}/\dot{Q}$ inequality. Positive differences indicate reduced gas exchange efficacy. Note that cross-current efficacy is always greater and that $O_2$ is affected more than $CO_2$
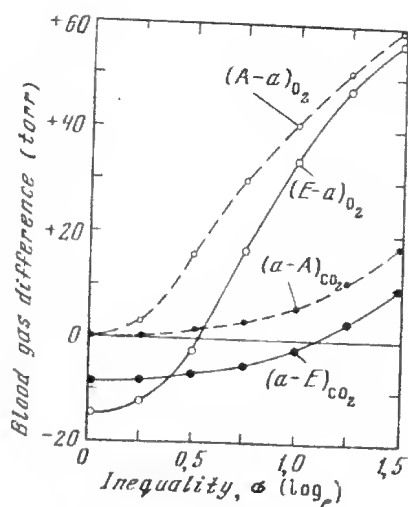


inequality the difference becomes more positive with both models but cross-current efficacy is always better (i.e. difference smaller) than alveolar. For uptake of a gas like $O_2$, the expired-arterial, or alveolar-arterial,difference is inversely proportional to efficacy. The cross-current difference is smaller than the alveolar difference at all levels of $\dot{V}/\dot{Q}$ inequality. Thus, the effects of inhomogeneity of $O_2$, $CO_2$ and inert gases are all qualitatively similar.

Figure 4 also shows that $O_2$ is more vulnerable than $CO_2$ to chronic $\dot{V}/\dot{Q}$ inequality (as might be expected from the acute effects described above). This is due to the difference in $O_2$ and $CO_2$ dissociation curves, similar to the different effects of $\dot{V}/\dot{Q}$ inequality on different inert gases depending upon their blood-gas partition coefficient. Of particular interest is the effect of the degree of $\dot{V}/\dot{Q}$ inequality measured in geese on $O_2$ and $CO_2$ exchange. At this level of inequality ($\sigma \approx 0.6$) expired-arterial $O_2$ differences are positive, and thus qualitatively indistinguishable from alveolar values. However, arterial expired $CO_2$ differences are still negative and clearly the result of cross-current gas exchange.

Such modeled blood-gas differences are qualitatively similar to values measured in normoxic birds (unpublished observations). However, quantitatively these predicted values do not agree with the observed values, particularly for $O_2$. Figure 5 shows results from 3 geese, in which $\dot{V}/\dot{Q}$ inequality was measured with the multiple inert gas elimination technique, blood $P_{O_2}$ and $P_{CO_2}$ were measured and blood $P_{O_2}$ and $P_{CO_2}$ were predicted. $P_{O_2}$ and $P_{CO_2}$ were predicted with the computer model of cross-current $O_2$ and $CO_2$ exchange considering $\dot{V}$ and $\dot{Q}$ to be distributed between parabronchi as was determined by the multiple inert gas elimination technique (vide supra). Predicted $O_2$ values were almost always greater than measured values but this was not the case for $CO_2$. Referring back to Figure 4, this would be seen as measured arterial-expired $CO_2$ differences falling on the curve at the appropriate level of $\dot{V}/\dot{Q}$ inequality but the expired-arterial $O_2$ difference would be more positive than indicated by the curve. This is in contrast to our ability to accurately predict arterial $P_{O_2}$ and $P_{CO_2}$ in resting mammals at sea level and may indicate a larger diffusion resistance for $O_2$ in avian lungs (Powell,
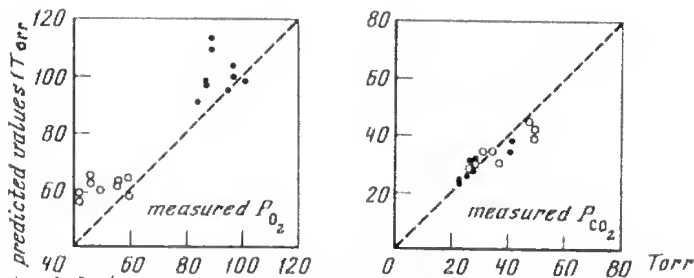
F i g. 5. Arterial (solid symbols) and mixed venous (open symbols) $P_{O_2}$ and $P_{CO_2}$ predicted for the degree of $\dot{V}/\dot{Q}$ inequality measured in 3 geese as a function of the measured values. The predictions are based on $O_2$ and $CO_2$ dissociation curves measured in geese. Predictions are good for $O_2$, but not $CO_2$ and are in a direction indicating that diffusion equilibrium may not be occurring for $O_2$ as the model assumes

1982). Recall that the model assumes diffusion equilibrium, which is valid for inert gases but may not be for $O_2$. Also, inhomogeneous blood flow along a parabronchus can affect $O_2$ exchange, unlike inert gases, but the effect is very small (Holle et al., 1978; Powell, 1982). These two factors may be involved in depressing arterial $P_{O_2}$ in birds.

PHYSIOLOGICAL SIGNIFICANCE

In answer to our original question, it appears that gas exchange efficacy is reduced from ideal levels more in avian lungs that it is in mammalian lungs. This is because there is more inequality, not because cross-current gas exchange is more susceptible to effects of $\dot{V}/\dot{Q}$ inequality per se. However, the avian lungs start out with an advantage - efficacy of ideal cross-current lungs is greater than ideal alveolar lungs - so the end result is similar gas exchange efficacy in birds and mammals.

The net effect at rest and sea level is similar arterial $P_{O_2}$ in birds and mammals but lower arterial $P_{CO_2}$ in birds. Lowered arterial $P_{CO_2}$ has been shown to be important for maintaining arterial $P_{O_2}$ in mammals at high altitude (West, Wagner, 1981). The abilities of birds at high altitude are well documented (cf. Black, this volume) but evolutionary pressures for high altitude flight were probably small so other consequences of the low cross-current arterial $P_{CO_2}$ may be more important (e.g. acid-base regulation). Alternatively, $P_{CO_2}$ differences may be only incidental. Mammals could easily lower their arterial $P_{CO_2}$ to avian levels by mild hyperventilation (Scheid, personal communication).

If one considers a minimum arterial $P_{O_2}$ is necessary for survival then more efficient gas exchange, like that provided by the cross-current model, may be required for heterogeneous lungs. The larger amount of $\dot{V}/\dot{Q}$ inequality in avian compared to mammalian lungs may be a direct consequence of heterogeneous partitioning. Flow through ventilation of the avian lung by air sacs acting as bellows might be inherently less uniform than tidal ventilation in alveolar lungs. The advantages of cross-current exchange may offset such possibly unavoidable functional inhomogeneities.

Once the structural and functional basis for the measured $\dot{V}/\dot{Q}$ inequality in avian lungs is better understood, there may be further insights. For ex-

ample, if $\dot{V}/\dot{Q}$ inequality is under some sort of physiological control then it may be reduced under conditions like exercise or high altitude. A full understanding of the significance of the unique structure and function of avian lungs awaits not only complete descriptions of $\dot{V}/\dot{Q}$ inequality but other functional inhomogeneities (e.g. diffusion-perfusion mismatches) as well.

## SUMMARY

Evolution of endothermy and associated high metabolic rates required increased gas exchange surface area. This occurred by homogeneous partitioning of mammalian alveolar lungs and heterogeneous partitioning of the avian respiratory system. The "cost" of increased surface area by partitioning includes possible functional inhomogeneities. Inert gases offer a valuable tool to study this problem. Models show that cross-current gas exchange in avian lungs is not affected more than alveolar gas exchange by $\dot{V}/\dot{Q}$ inequality. Measurements of $\dot{V}/\dot{Q}$ inequality show more inhomogeneity in birds than in mammals. However, the superior efficacy of cross-current gas exchange in birds results in higher efficacy of inert gas elimination in birds. Models show the effects of $\dot{V}/\dot{Q}$ inequality of $O_2$ and $CO_2$ to be similar in cross-current and alveolar exchanges. However, $O_2$ exchange in avian lungs is impaired more than predicted by cross-current models of $\dot{V}/\dot{Q}$ inequality, indicating other factors (e.g. diffusion resistances) may impede gas exchange in birds. Thus, at least at rest and sea level, the inherently greater efficacy of avian lungs is reduced to a level similar to alveolar lungs.

## R e f e r e n c e s

Black C.P. Respiration and gas exchange at high altitude. (This volume).

Duncker H.R. - In: Respiratory Function in Birds, Adult and Embryonic / Ed. by J.Piiper. N.Y.: Springer-Verlag, 1978, p. 2-15.

Farhi L.E., Plewes J.L. - In: Pulmonary Gas Exchange. Vol. II / Ed. by J.B.West. N.Y.: Academic Press, 1980, p. 1-31.

Holle J.P., Heisler N., Scheid P. - Am. J. Physiol., 1978, 234, p.R146-154.

Kelman G.R. - J. Appl. Physiol., 1966, 21, p. 1375-1376.

Kelman G.R. - Respir. Physiol., 1967, 3, p. 111-115.

Mitchell G.S. , Gleeson T.T., Bennett A.F. - Am. J. Physiol., 1981, 240, p. R29-R37.

Perry S.F. - Respir. Physiol., 1978, 34, p. 61-81.

Piiper J., Scheid P. - In: Pulmonary Gas Exchange. Vol. I / Ed. by J.B.West. N.Y.: Academic Press, 1980, p. 131-171.

Powell F.L. - Fed. Proc., 1982.

Powell F.L., Wagner P.D. - Respir. Physiol., 1982a.

Powell F.L., Wagner P.D. - Respir. Physiol., 1982b.

Scheid P. See this volume.

Wagner P.D., West J.B. - In: Pulmonary Gas Exchange. Vol. I / Ed. by J.B.West. N.Y.: Academic Press, 1980, p. 219-262.

West J.B. - Respir. Physiol., 1969/70, 8, p. 66-85.

West J.B., Wagner P.D. - In: Bioengineering Aspects of the Lung / Ed. by J.B.West. N.Y.: Marcel Dekker, 1977, p. 361-457.

West J.B., Wagner P.D. - Respir. Physiol., 1980, 42, p. 1-16.

# AVIAN RESPIRATION IN THE SERVICE OF BODY TEMPERATURE REGULATION

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## INTRODUCTION

Ventilation in birds and mammals servss primarly in gas exchange, but
the passage of air  through the airways will inevitably also results in loss
of water and heat to the surrounding air. These exchanges will increase with
incrsased temperature difference between the deep body and the ambient air.
Heat loss from the respiratory tract is the most important avenue for evapo-
rativs heat loss at high ambient temperatures in birds and mammals practic-
ing panting.

The present review attempts to evaluate our present knowledge of some of
the ways in which changes in ventilatory pattern serves the body temperature
regulation in birds. See Dawson (1982) for a more extensive review of the
evaporative watsr loss in birds.

## EXPOSURE TO HIGH AMBIENT TEMPERATURES

Exposed to high ambient temperatures. birds typically increase the venti-
lation of the upper respiratory tract as the only regulated response for in-
creasing the rate of evaporative cooling. This increase may be due to gular
fluttering and/or panting.

Gular fluttering consists of rapid movements of the buccal floor, often
at frequencies synchronous with the panting frequency (Lasiewski, 1972).
Weathers and Schoenbaechler (1976) reported that evaporative cooling contri-
buted by gular fluttering accounted for 20% of the total evaporative water
loss in the Japanese quail (Coturnix coturnix). In the Domestic fowl (Gallus
gallus)  35% of the total water loss during panting could be attributed the
gular pump (Brackenbury et al., 1981b). Although gular fluttering is of com-
mon occurrence in many non-passerine species, the studies on the Japanese
quail and Domestic fowl appears to be the only ones offering quantitative
data on ths importance of gular fluttering for the total evaporative heat
loss. Similar studies in species of the Caprimulgids, Cormorants, and Peli-
cans, for which gular fluttering by observations seems to be conspicuous,
would liksly prove rewarding. An attempt has been made by Lasiewski (1969),
who found that the gular fluttering in the Poorwill (Phalaenptilus nuttallii)
probably contribute more than half of the total evaporativs watsr loss at
ambient temperatures above 39.5°C.

Panting as a source of evaporative cooling have been observed in nearly
all species of birds studied (Salt, 1964; Richards, 1970; Calder, King, 1974).
Panting results in sevsral-fold increases in total  ventilation, but very
few studies have involved direct measurement of tidal volume (Bech et al.,
1979). Fig. 1 illustrates changes in breathing frequency and tidal volume
and the resultant effect on total ventilation. Typically ventilation in-
creases 2.5 to 6 times the non-panting value, the result of a 10- to 30-fold
increase in breathing frequency and a simultaneous decrease in tidal volume
to between 15 and 40% of the non-panting valus.
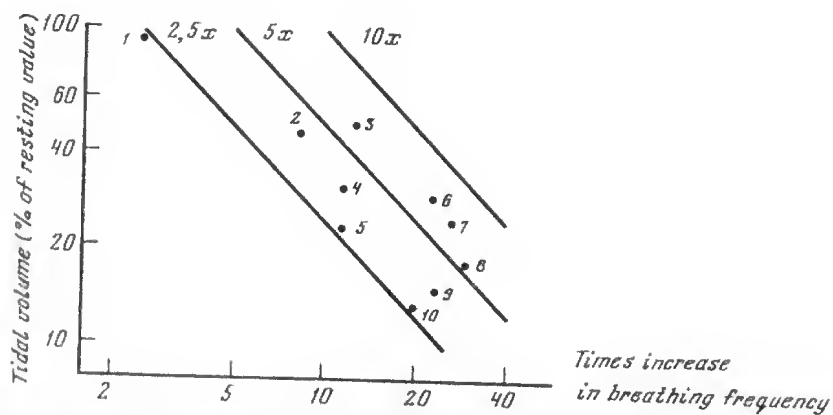
F i g. 1. Relationship between respiratory frequency (as a multiple of the non-panting value) and the tidal volume (expressed as a percentage of the non-panting value) during panting in birds. The lines show isopleths for total ventilation-increases during panting. 1 – Fulica atra (Brent et al., 1982), 2 – Anas platyrhynchos (Bretz, Schmidt-Nielsen, 1971), 3 – Geococcyx californianus (Calder, Schmidt-Nielsen, 1967), 4 – Bolborhynchus lineola (Bucher, 1981), 5 – Gallus gallus (Brackenbury et al., 1981), 6 – Columba livia (Calder, Schmidt-Nielsen, 1966), 7 – Anas platyrhynchos (Bouverot et al.,1974),8.–Cygnus olor (Bech, Johansen, 1980), 9 – Phoenicopterus ruber (Bech et al., 1979), 10 – Columba livia (Remirez, Bernstein, 1976)

The marked increase in ventilation volume associated with panting subjects the birds to the risk of a respiratory alkalosis. To avoid this it has been suggested that birds are able to shunt portions of the ventilated air away from the parabronchial gas-exchange surfaces during hyperventilation (Zeuthen, 1942; Marder et al., 1974; Marder, Arad, 1975; Krausz, 1977). However, no anatomical evidence for such a shunt mechanism have been presented. Instead, recent experiments have suggested three .ifferent panting patterns which may offer protection against overventilation of the gas exchange surfaces of the lung. These different patterns are schematically illustrated in Fig. 2.
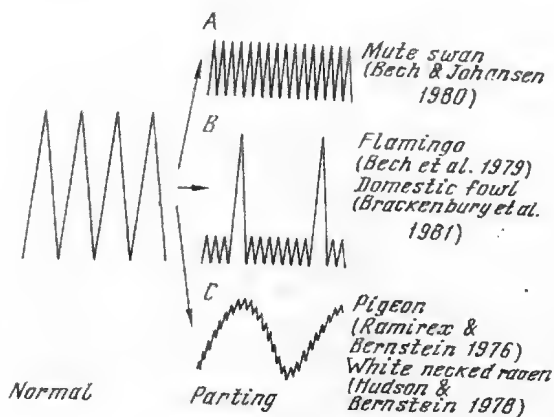


F i g. 2. Schematic illustration of the three different patterns of panting found in birds

In the simplest form (Fig. 2, A), which have been described in the Mute swan (Cygnus olor) (Bech, Johansen, 1980), the hyperthermic breathing is characterized by a high breathing frequency and a constant low tidal volume. Each tidal volume typically is only slightly larger than the anatomical dead space. Calculations show that the parabronchial ventilation during this panting pattern is held at the pre-panting level despite a 5.4-fold increase in total ventilation (Bech, Johansen, 1980).

Another pattern (Fig. 2, B), termed the "flush-out" panting, consists of a high frequency, low tidal volume pattern, with tidal volume equal to or smaller than the anatomical dead space. At regular intervals a few very deep breathing movements occur. These regularly occurring "flush-outs" serve to maintain parabronchial gas exchange, while the high frequency breathing primarly subserves the need for convective air flow to promote evaporative cooling. Flush-out panting was first described in the Greater flamingo (Phoenicopterus ruber) by Bech et al. (1979) and have recently also been reported for the Domestic fowl by Brackenbury et al. (1981a).

A third panting pattern (Fig. 2, C) involves a stable and very high breathing frequency with tidal volumes smaller than the dead space. Parabronchial ventilation is produced by alternating imbalances between the inspiratory and expiratory volumes such that the parabronchial surfaces become ventilated at a lower frequency than the actual panting rats. This pattern has been termed "compound" panting and has been reported to occur in the Pigeon (Columba livia) (Ramirez, Bernstein, 1976; Bernstein, Samaniego, 1981) and the White-necked raven (Corvus cryptoleucus)(Hudson, Bernstein, 1978).

All the described patterns of hyperthermic panting have been demonstrated to be associated with small or no respiratory alkalosis as evidenced by nearly stable arterial pH (Bech et al., 1979; Bech, Johansen, 1980; Bernstein, Samaniego, 1981).

Recent data (Brent et al., 1982) on ventilation in the European coot (Fulica atra) have shown that lung oxygen extraction decrease markedly when birds are exposed to an ambient temperature of 35°C (Table 1). In spite of a more than doubling of the parabronchial ventilation at 35°C, the $O_2$-uptake increase only slightly. This situation correlates with a reduction in the parabronchial oxygen extraction to only 13.9%, compared to 27.0% at an ambient temperature of 30°C. Bucher (1981) also reported lung oxygen extraction in the Linneated parakset (Bulborhynchus lineola) to decrease during panting.

A regulated alteration of parabronchial $O_2$-extraction offers obvious advantages for body temperature regulation. It enables birds to increass lung ventilation during panting without a resulting respiratory alkalosis,because the reduced $O_2$-extraction balances the elevated ventilation with respect to overall respiratory gas exchange.

The mechanism behind the changes in oxygen extraction remain unknown. Based on anatomical evidence a ventilation-shunt seems unlikely. Changes in parabronchial perfusion, either in the form of discrets shunts or an alterated regional blood perfusion are probably participating factors. Parry and Yates (1979) indeed found a change in regional blood perfusion of the parabronchi during panting in the Domestic fowl but not in the pigeon. In the fowl the

ventral segments of the paleopulmonic parabronchi were relatively less per-
fused during panting. Since blood flow to the parabronchi decreases from the
dorsal to the ventral part of the parabronchi in non-panting birds (Holle et
al., 1978; Parry, Yates, 1979), the perfusion-changes found during panting
in the fowl will likely cause a further ventilation-perfusion inequality in
the lung and thereby tend to decrease the gas exchange efficiency (Scheid,
Holle, 1978). Whether a similar change in regional lung perfusion is occurring
in the coot at high ambient temperatures is unknown, but studies are in
progress to establish the nature of the mechanism responsible for the con-
spicuous temperature induced changes in lung oxygen extraction.

It have earlier been advocated that some birds, particularly arctic and
montane species, do not practice panting at high ambient temperatures (Salt,
1964). However, no study includes direct measurements of tidal volume and
breathing frequency in these species. It can be argued that _Fulica_ only prac-
tices a limited form of panting (Brent et al., 1982). Fig. 1 shows that tidal
volume is nearly unchanged during panting at 35°C causing the augumentation of
the total ventilation to be proportional to the increased breathing frequen-
cy. At higher ambient temperatures (40°C) _Fulica_ increased the breathing fre-
quency still further, but when this happened the birds became severely hyper-
thermic. The species would thus not tolerate exposure to 40°C for more than a
few hours. At 35°C ambient temperature the lung oxygen extraction may have
reached a maximum possible reduction, and any further increase in total ven-
tilation might result in hypercapnia and alkalosis, because the parabronchial
ventilation increases in parallel with the increase in total ventilation. The
strictly aquatic habitat of the coots suggests a lesser dependance on respira-
tory evaporative cooling than that of convective heat loss from the webbed
feet (Brent et al., 1982).

Similarly, MacMillen (1974) reported two species of Hawaiian honeycreepers
(_Drepanididae_) to have a very inefficient evaporative cooling capacity. At
ambient temperatures of 38-39°C these species were only able to dissipate
about 50 to 60% of their total heat production, and for one of the species,
an ambient temperature of 40°C was found to be lethal. The marked reduction in
high temperature tolerance in these species is probably related to their nor-
mal habitat, which is the high forest region, where the ambient temperature
probably never exceeds thermal neutrality for honeycreepers (MacMillen, 1974).

Thomas and Robin (1977) reported that the desert-living sandgrouse, _Pte-_
_rocles alchata_, did not use panting during incubation in the open sun, where
air temperature reached values exceeding 50°C. Instead these birds apparently
used gular fluttering and "beak gaping". However, the authors did only vi-
sually observe the birds from a distance, and a more detailed study is
needed to confirm the absence of panting in the sandgrouses.

## EXPOSURE TO LOW AMBIENT TEMPERATURES

At ambient temperatures below the thermoneutral zone birds have to in-
crease the heat production and/or to reduce heat loss in order to keep the
deep body temperature stable.

Similar to what has been found for many mammals, a decrease in exhaled
air temperature relative to body temperature has been recorded for several

avian species exposed to decreasing ambient temperatures (Schmidt-Nielsen et al., 1970; Murrish, 1973; Brent et al., 1982). The amount of heat and water recovered by decreasing the exhaled air temperature may exceed 85%. So far, there seems to be no clear relationship between either body size, habitat or general behaviour and the capacity to decrease exhaled air temperature.

In addition to the obvious advantage of a reduced expired air temperature for heat conservation, further prevention of heat loss could be obtained if the total volume of air ventilated could be reduced in relation to the aerobic oxygen requirement of the species (i.e. a reduction in the ventilatory requirement). This form of heat conservation is clearly operating in the coot, expressed by a marked increase in parabronchial $O_2$-extraction. Table 1 shows that the oxygen extraction in the coot changes from 28.4% at thermoneutrality to 62.0% at an ambient temperature of -25°C (Brent et al., 1982). The benefit of this change is striking. At -25°C the aerobic $O_2$ requirement can be maintained by only 50% of the parabronchial ventilation which would have been necessary if the $O_2$-extraction had remained unchanged. In addition to the change in oxygen extraction, the coots lower the exhaled air temperature, at -25°C to about 0°C. Calculations show that this brings total heat conservation at -25°C to about 90% of the heat added to the air at inspiration. About 79% can be accounted for by the lowered exhaled air temperature and 11% by the increased oxygen extraction. At -25°C the amount of heat recovered by the increased oxygen extraction is 2.6% of the total heat production. Although this appear of limited importance, it actually implies a reduction of the respiratory heat loss by more than 50%. An additional bonus ooncerns water conservation since the increased $O_2$-extraction also reduced the respiratory water loss by more than 50% (Brent et al., 1982). Bucher (1981) found the oxygen extraction in the Linneated parakeet to increase from 29% at thermoneutrality to about 37% at 5°C, at which temperature the change in oxygen extraction accounted for a reduction in the heat and water loss of 21%.

Bernstein and Schmidt-Nielsen (1974) did not find any significant changes in oxygen extraction in the Fish crow (Corvus ossifragus) at ambient temperatures between 5°C and 25°C, although their data suggest a small increase at the lowest ambient temperature. In the Pigeon, the oxygen extraction remained unchanged between 2°C and 22°C (Bouverot et al., 1976).

The study on the European coot (Brent et al., 1982) is the first which

T a b l e  1. Oxygen uptake (2 - ml $O_2$ kg$^{-1}$min$^{-1}$), parabronchial ventilation (3 - ml kg$^{-1}$min$^{-1}$),and parabronchial $O_2$-extraction (4 - %) in the European coot (Fulica atra) at various ambient temperatures (1 - °C). From Bernt et al., 1982

| 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
|-----|------|-------|------|------|------|-------|------|
| -25° | 61.8 | 476.0 | 62.0 | 20° | 18.2 | 305.9 | 28.4 |
| -10° | 47.2 | 483.0 | 46.6 | 25° | 18.2 | 316.0 | 27.5 |
| 0° | 37.5 | 430.0 | 41.6 | 30° | 18.3 | 324.0 | 27.0 |
| 10° | 27.8 | 374.0 | 35.5 | 35° | 20.1 | 691.2 | 13.9 |
| 15° | 22.9 | 326.8 | 33.4 | | | | |

give information on ventilatory data and oxygen extraction at ambient temperatures below 0°C, and further studies are much needed in order to establish if a reduction in the ventilatory requirement (i.e. increased oxygen extraction) during cold exposure has general validity in birds.

The mechanism underlying the increased lung oxygen extraction at ambient temperatures below the thermoneutral zone can only be surmised. Studies in the domestic duck have shown that the physiological perfusion- and ventilation-shunts amounts to 2.7% and 9.4% respectively at thermoneutral conditions (Burger et al., 1979). A decrease in these shunts might be one way of increasing the efficiency of the parabronchial gas exchanger.

R e f e r e n c e s

Bech C., Johansen K. - J. exp. Biol., 1980, 88, p. 195-204.
Bech C., Johansen K., Maloiy G.M.O. - Physiol. Zool., 1979, 52, p. 313-328.
Brackenbury J.H., Avery P.,Gleeson M. - J. exp. Biol., 1981a, 90, p. 343-345.
Brackenbury J.H., Avery P., Gleeson M. -J.comp. Physiol.,1981b, 145,p.63-66
Bernstein M.H., Semaniego F.C. - Physiol. Zool., 1981, 54, p. 308-315.
Bernstein M.H., Schmidt-Nielsen K. - Resp. Physiol., 1974, 21, p. 393-401.
Bouverot P., Hildwein G., Oulhen P. - Resp. Physiol., 1976, 28, p. 371-385.
Bouverot P., Hildwein G., LeGoff D. - Resp. Physiol., 1974, 21, p. 225-269.
Brent R., Pedersen P.F., Bech C., Johansen K. -J.exp. Biol.,1982,54,p.103-118.
Bucher T. - J. comp. Physiol., 1981, 142, p. 479-488.
Burger R.E., Meyer M., Graf W., Scheid P. - Resp. Physiol., 1979, 36, p.19-37.
Calder W.A., King J.R. - In: Avian Biology. Vol. 4 / Eds. D.S.Farner,
    J.R.King. N.Y.: Academic Press, 1974, p. 259-413.
Calder W.A., Schmidt-Nielsen K. - Proc. natn. Acad. Sci.USA,1966,55, p.750-756.
Calder W.A., Schmidt-Nielsen K. - Amer. J. Physiol., 1967, 213, p. 883-889.
Dawson W.R. - Comp. Biochem. Physiol., 1982, 71A, p. 495-509.
Holle J.P., Heisler N., Scheid P. - Amer. J. Physiol., 1978, 234, p.R146-R154.
Hudson D.M., Bernstein M.H. - Fed. Proc., 1978, 37, p. 472.
Krausz S., Bernstein R., Marder J. - Comp. Biochem.Physiol,1977,57A, p.245-247
Lasiewski R.C. - Amer. J. Physiol., 1969, 217, p. 1504-1509.
Lasiewski R.C. - In: Avian Biology. Vol. 2. N.Y. 1972, p. 287-342.
MacMillen R.E. - Condor, 1974, 76, p. 62-69.
Marder J., Arad Z. - Comp. Biochem. Physiol., 1975, 51A, p. 887-889.
Marder J., Arad Z., Gafni M. - Physiol. Zool., 1974, 47, p. 180-189.
Murrish D.E. - Resp. Physiol., 1973, 19, p. 262-270.
Parry K., Yates M.S. - Resp. Physiol., 1979, 38, p. 131-140.
Ramirez J.M., Bernstein M.H. - Fed. Proc., 1976, 35, p. 2562-2565.
Richards S.A. - Biol. Rev., 1970, 45, p. 223-264.
Salt G.W. - Biol. Rev., 1964, 39, p. 113-136.
Scheid P., Holle J.P. - In: Respiratory function in birds, adult and embryon-
    ic / Ed. by J.Piiper. B.: Springer-Verlag, 1978, p. 105-111.
Schmidt-Nielsen K., Hainsworth F.R., Murrish D.E. - Resp. Physiol., 1970,
    2, p. 263-276.
Thomas D.H., Robin A.P. - J. Zool. (L.), 1977, 183, p. 229-249.
Weathers W.W., Schoenbaechler D.C. - J. Appl. Physiol., 1976, 40, p. 521-524.
Zeuthen E. - Kgl. Dan. Vid. Selsk. Biol. Medd. XXII, 1942, p. 1-51.

## SIGNIFICANCE OF LUNG STRUCTURE FOR PERFORMANCE AT HIGH ALTITUDE

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INTRODUCTION

Barometric pressure ($P_B$) drops in an exponential fashion with elevation above sea level. Since the fractional concentration of oxygen remains nearly the same at all altitudes, environmental $O_2$ partial pressure ($P_{O_2}$) drops in proportion to $P_B$. Inspired partial pressure at body conditions, $PI_{O_2}$, is even lower due to the humidification at the body temperature.

Only few mountaineers have yet been able to climb Mt.Everest, the highest elevation on earth (8848 m), without supplemental $O_2$. Inspired $P_{O_2}$ ($PI_{O_2}$) at that altitude is 42 Torr, and arterial $P_{O_2}$ ($Pa_{O_2}$) for man breathing air on Mt. Everest may be estimated at 22 Torr (Dejours, 1982). Apparently, this elevation sets an upper limit for man, even if well-adapted to high altitude, when breathing air. It is likely that other mammals do not perform much better at high altitude than does man. Birds, on the other hand, have been observed flying at substantially higher altitudes. In fact, the bar-headed goose (Anser indicus) regularly migrates from the Indian subcontinent across the Himalayan Mountains to breed on large lakes throughout the south-central reagions of Asia; one flock has been observed passing right over Mt. Everest (cf. Black, Tenney, 1980). The altitude record, however, is held by an African vulture (Gyps ruepellii) that collided with an airplane while soaring at 11,300 m (Laybourne, 1974).

It may be asked to what extent differences in the gas exchange efficiency between the mammalian and avian lungs (cf. Scheid, 1979), deriving from differences in lung structure, are responsible for the apparent differences in high altitude tolerance between mammals and birds.

GAS EXCHANGE EFFICIENCY

Substantial differences exist in the structural arrangement between the mammalian and the avian lung as elaborated in the contribution of Piiper and Scheid to this Symposium. For gas exchange, the most conspicuous differences reside in the structure of the functional lung unit: the alveolus for mammals, the parabronchus for birds. The alveolus may be viewed as a well-mixed pool of (alveolar) air that is contacted by blood in the pulmonary capillaries. The parabronchus constitutes a tube, open at both ends, through which ventilatory air passes to contact blood in capillaries all along the tube.

Piiper and Scheid(1975) have assigned functional models to these structural systems which allowed a comparative analysis of gas exchange in both systems. Their analysis suggested the following features:

1. The amount of gas exchanged per unit time in both systems depends on ventilation, blood flow, diffusing capacity (representing the gas conductance of the gas/blood separating membrane), on physical properties of the gas under study, and their partial pressures in air and blood entering the lung.

2. Given these parameters, the gas exchange efficiency is higher for the cross-current model of the avian parabronchial lung than for the mammalian

976

alveolar lung. In particular, for a given $O_2$ uptake and for given inspired $P_{O_2}$ ($PI_{O_2}$), arterial $P_{O_2}$ ($Pa_{O_2}$) is higher in the parabronchial lung.

This offers the possibility that birds can endure higher altitudes (lower $PI_{O_2}$) because the higher gas exchange efficiency of their lung ensures sufficiently high $Pa_{O_2}$ even at the higher altitude.

Measurements performed on the Bar-headed Goose (Anser indicus) at simulated altitudes of about 9,000 m showed indeed significantly higher $Pa_{O_2}$ values (Black, Tenney, 1980) than those estimated for man (see above).

EFFECT OF LUNG STRUCTURE

To estimate the effect of lung structure on high altitude tolerance, the data presented by Dejours (1982) have been used. His values for ventilation, blood flow, diffusing capacity and blood transport properties (e.g. slope of $O_2$ dissociation curve) have been employed in a calculation based on the cross-current model. In this calculation, the $PI_{O_2}$ was obtained which gave the same $Pa_{O_2}$ level as that observed in man. The question investigated was thus: What degree of reduction in $PI_{O_2}$ can man afford, without a change in $Pa_{O_2}$, when his alveolar lung is replaced by a parabronchial lung?

The calculation yielded a reduction of $PI_{O_2}$ from 42 to 37 Torr. This reduction in the $PI_{O_2}$ corresponds to a gain in the maximum tolerated altitude by about 780 m to somewhat over 9,600 m.

CONCLUSION

Although this gain in altitude is significant, the maximum altitude reached by birds is still far in excess of 9,600 m. In fact, Black and Tenney (1980) have subjected bar-headed geese to simulated altitudes of 11,600m with only mild signs of malfunction. At this altitude, $PI_{O_2}$ is below 25 Torr, and $Pa_{O_2}$ only a few Torr lower.

We would then conclude that

1) Lung structure contributes significantly to the high altitude performance of birds in that the avian parabronchial lung displays a particularly high gas exchange efficiency.

2) Other factors contribute to the extraordinary high-altitude tolerance that some avian species display. Recent experiments of Grubb et al.. (1977) suggest that the absence of hypocapnic vasoconstriction of cerebral vessels play a significant role.

SUMMARY

High altitude is characterized by low environmental oxygen partial pressure ($P_{O_2}$). While only few human subjects have been able to climb Mt. Everest (altitude, 8848 m; $P_{O_2} \approx 42$ Torr) without additional $O_2$, several bird species tolerate even higher altitudes. The effect of lung structure, and particularly of the higher gas exchange efficiency of the avian parabronchial compared with the mammalian alveolar lung, has been estimated by calculating to what altitude man could climb when equipped with a parabronchial lung. For the same arterial $P_{O_2}$, man equipped with parabronchial lungs could afford a 5 Torr reduction in ambient $P_{O_2}$, corresponding to a gain in height of about 780 m. Thus, the higher gas exchange efficiency of the avian lung can account for a significant increase in high altitude tolerance; however, this cannot account entirely for the apparent high altitude tolerance of birds.

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# RECENT ADVANCES IN UNDERSTANDING THE CONTROL OF BREATHING IN BIRDS

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## INTRODUCTION

The respiratory control system adjusts ventilation of the gas exchange regions of the lung so as to eliminate excess carbon dioxide produced by increased metabolism, or to conserve carbon dioxide at some present level when metabolic rate is low. There are at least three categories of factors that influence the central respiratory controller to produce a neural output to respiratory muscles in accordance with metabolic or heat exchange requirements. These include: 1) chemogenic factors, which involve chemical changes in the body; 2) thermogenic factors, which result from changes in the external and internal thermal environment; and 3) neurogenic factors, which arise from activation of higher brain centers and/or from stimulation of receptors in muscles, tendons and other regions of the body. This review discusses the current state of knowledge about the influence of each of these factors on the control of breathing in birds during rest and exercise.

## CHEMOGENIC FACTORS IN THE CONTROL OF BREATHING

1. Chemical stimuli. Three principal chemical stimuli known to change the magnitude and pattern of ventilation are: 1) Changes in the partial pressure of $O_2$ in the arterial blood ($PaO_2$); 2) Changes in the partial pressure of $CO_2$ in the arterial blood ($PaCO_2$) and in the intrapulmonary gas; and 3) Changes in the hydrogen ion concentration in the arterial blood, $/H^+/a$. In addition, other chemicals may be produced by increasing metabolic activity in muscle or other regions of the body. These stimuli appear to reflexly activate negative feedback mechanisms that attempt to prevent marked changes in arterial $PO_2$, $PCO_2$, and pH despite changes in the activity patterns of the birds.

2. Chemoreceptors. The chemical stimuli are detected by chemoreceptors whose afferent neurons project to the central nervous system. These chemoreceptors are located in several regions of the body and appear specialized to detect specific stimuli.

One of the most studied organs containing chemoreceptors is the carotid body. A carotid body is situated on each side of the bird caudal to the thyroid gland in the thoracic cavity, on or near the carotid or caudal thyroid artery (de Kock, 1958; Dreyer et al., 1977) from which it receives its blood supply. Innervation is supplied by small nerves leaving the nodose ganglion of the vagus nerve. Cells within the carotid body possess afferent, efferent, and reciprocal synapses. Two or three cell types (Type I, II, and III) are present (Kobayashi, 1969; Kobayashi, 1971; Hodges et al., 1975; King et al., 1975; Dreyer et al., 1978) but it is still not known if one of these cell types is the receptor cell or exactly how the afferent neurons are activated. Current evidence suggests that the carotid body is the only receptor system in the bird which senses low partial pressure of $O_2$ (Bouverot et al., 1974b; Bouverot, 1978; Bouverot et al., 1979). The afferent discharge from this organ increases when arterial $PO_2$ is lowered and is suppressed by elevating $PaO_2$ by inhaling high concentrations of $O_2$ (Bouverot, Leitner, 1972). This

receptor may also have some sensitivity to $PaCO_2$, but its sensitivity to that gas appears to be relatively low (Bouverot et al., 1974b).

All birds studied thus far by using neurophysiological techniques have been shown to possess a very sensitive receptor system in their lungs that responds to change in intrapulmonary $CO_2$ concentration (Fedde, Kuhlmann,1978). These intrapulmonary chemoreceptors (IPC) appear to be located in the gas exchange region of the lungs (Scheid et al., 1974; Nye, Burger, 1978; Crank et al., 1980) and unlike mammalian carotid body chemoreceptors, they increase their discharge frequency as intrapulmonary $CO_2$ concentration is reduced (Fedde, Peterson, 1970; Fedde et al., 1974a). Because of the wide fluctuations in intrapulmonary $CO_2$ concentration in the bird lung with each breath, these receptors alter their discharge during each respiratory cycle with high discharge frequency during inspiration and lower discharge frequency during expiration (Fedde, Scheid, 1976). These receptors can be stimulated either by inhaling $CO_2$ or by changing the $PCO_2$ in the venous blood returning to the lungs (Fedde et al., 1982). The IPC also have some sensitivity to /$H^+$/ (Powell et al., 1978). The exact mechanism by which $CO_2$ or $H^+$ alter the discharge of these receptors is not known, but their sensitivity to $CO_2$ is markedly reduced after administering the carbonic anhydrase inhibitor, acetazolamide (Scheid et al., 1978).

Receptors sensitive to $CO_2$ also appear to be present in the brain of birds (Sébert, 1978, 1979; Milsom et al., 1981). Reports vary as to the sensitivity of these receptors and further studies will be required to determine their location and importance in the respiratory control system.

So far, it is not known if chemoreceptors exist in muscles or other tissue that might be stimulated by chemicals resulting from altered metabolism during exercise. Such receptors, if they exist, might be involved in the hyperpnea of exercise.

3. <u>Ventilatory responses to stimulation of various chemoreceptors.</u> In most cases, ventilation has been studied during rest, either in awake, anesthetized, or decerebrate birds, when various chemoreceptors have been stimulated. Most recently, however, techniques have been devised to study the action of these chemoreceptors on the control of breathing during exercise. Results during rest and exercise will be discussed.

Lowering the inspired $O_2$ concentration to values of below 12% in the resting bird causes a marked increase in ventilation (Fedde, 1976). Although tidal volume usually increases, in most cases, the majority of the ventilatory increase results from a rise in respiratory frequency. Removal of the carotid body abolishes the ventilatory response to hypoxia or hyperoxia so it is likely that the carotid body is responsible for detection of this stimulus (Bouverot et al., 1974b).

In exercising ducks, elevations in $PaO_2$ also reduce the ventilatory effort (Fig. 1a). That reduction is even more prominent if the duck is made hypoxic prior to elevating $PaO_2$ (Fig. 1b). It thus appears that the carotid body has a significant influence on the central respiratory controller during various metabolic states.

In the resting state, when $PCO_2$ is elevated in the arterial blood or in the gas within the lung, ventilation is markedly stimulated, usually by an increase in tidal volume (Fedde, 1976). That response has been obtained when
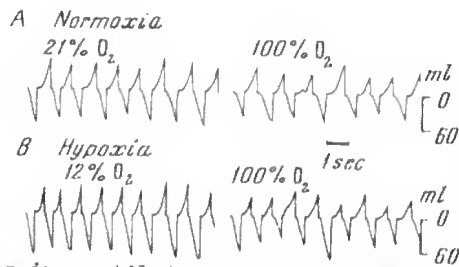
F i g. 1. Changes in ventilatory pattern of a Pekin duck running on a tread-mill (1.44 km·hr$^{-1}$ at a 3° incline) when allowed to breath 100% $O_2$. A, in-itially breathing air (minute ventilation, 2858 ml·min$^{-1}$) followed by 100% $O_2$ (minute ventilation, 2077 ml·min$^{-1}$); B, initially breathing hypoxic gas containing 12% $O_2$ (minute ventilation, 4438 ml·min$^{-1}$) followed by 100% $O_2$ (minute ventilation, 2992 ml·min$^{-1}$). Inspiration is from the center of the tracings down and the calibrations indicate inspiratory tidal volume

$CO_2$ is inhaled or $PCO_2$ elevated in the mixed venous blood (Boon et al., 1980). This response can result from altered activity of IPC alone (Fedde et al., 1982), but receptors in the carotid body and brain also may be involved.

During exercise, birds hyperventilate, as indicated by a reduction in $PaCO_2$ and in the $CO_2$ concentration in the clavicular and abdominal air sac (Butler et al., 1977; Torre-Bueno, 1978; Kiley et al., 1979; Brackenbury et al., 1981; Bech, Nomoto, 1982). Such a response should reduce the ventilatory drive from carotid body and central chemoreceptors, and increase the central inhibition from increased discharge of the IPC. Therefore, these receptors are not likely to be responsible for the hyperpnea of exercise. The IPC, and perhaps also carotid body and central chemoreceptors, may be acting to limit the degree of hyperventilation during exercise, thereby preventing severe respiratory alkalosis.

THERMOGENIC FACTORS IN THE CONTROL OF BREATHING

1. Thermal stimuli. Although most studies have concentrated on the ef-fects of elevated environmental temperature on the respiratory control sys-tem, both heating and cooling of the brain and spinal cord have been used to identify regions of the central nervous system important in thermal regulation.

2. Thermoreceptors. Receptors sensitive to thermal changes are present in the skin, spinal cord, and brain of birds. Current evidence suggests that stimulating peripheral thermoreceptors will not elicite panting unless cent-ral receptors are also activated (Richards, 1970). However, peripheral ther-moreceptors may provide a facilitating or inhibiting influence on the thermal response.

Available evidence indicates that a pacemaker in the midbrain or rostral pons is the dominant frequency controller in panting (Richards, Avery, 1978), but thermoreceptors in the spinal cord and hypothalamus may act to initiate or inhibit panting (Rautenberg et al., 1978).

3. Ventilatory responses to stimulation of thermoreceptors. Polypnea is the result of increases in environmental temperature. It may occur without causing hypocapnia in some birds (Schmidt-Nielsen et al., 1969; Bouverot et al.,1974a), but usually produces a reduction in $PaCO_2$ in the chicken (Lins-

980

ley, Burger,1964; El Hadi, Sykes, 1982). There is a strong interaction in the chicken between the chemoreceptor drive to ventilation and the thermo-receptor drive (Mather et al., 1980; Barnas et al.,1981). As polypnea causes a lower intrapulmonary and arterial $PCO_2$, the central respiratory controller is allowed to cycle faster and tidal volume becomes smaller. If the chicken is heat loaded but hypocapnia and alkalosis are not allowed to occur, the degree of polypnea is significantly reduced. Thus, at least in the chicken, hypocapnia and alkalosis appear to be required before the small tidal volume associated with panting can occur. Reduction in tidal volume may be desirable to prevent severe hypocapnia while maximizing ventilation of the dead space, and thereby maximizing heat loss by evaporation of water from the upper part of the respiratory tract.

During exercise, heat production is markedly increased. When ducks run on a treadmill at room temperature ($22°C$), body temperature rises by as much as $2°C$ in 20 minutes (Kiley et al., 1979). That is accompanied by a pronounced increase in respiratory frequency (up to 160 breaths·$min^{-1}$) and a reduced tidal volume (approximately 50% of rest). The birds hyperventilate and arte-rial $PCO_2$ may drop by as much as 5-8 Torr. However, if ducks are exercised at the same work load in a cold environment ($-5°C$) so that body temperature does not rise, the pattern of breathing is quite different. Tidal volume does not decrease appreciably and respiratory frequency increases to only about 60 breaths·$min^{-1}$. This response is accompanied by a hypocapnia of only about 3 Torr. It is clear that the hyperthermic drive to breathing alters the ven-tilatory pattern during exercise as well as during rest but is not the sole cause of the exercise hyperpnea in birds.

## NEUROGENIC FACTORS IN THE CONTROL OF BREATHING

1. _Mechanical stimulation_. Mechanical stimuli are presented to most body parts when the tissues are distorted and are especially prominent during exercise. Such stimuli may be continuously present or present only during movement of organs. The effects of mechanical stimuli on specific receptors involved in the control of breathing have not been extensively studied.

2. _Mechanoreceptors._ Recent experiments in chickens (Ballam et al.,1981a, b) have demonstrated that mechanoreceptors, stimulated by changes in body volume have an influence on the ventilatory pattern. It is known that affe-rent fibers from mechanoreceptors course centrally in the vagus nerve (Fedde et al., 1974b), but, with exception of mechanoreceptors in the gizzard (Duke et al., 1977) and the heart (Estavillo, Burger, 1973), the location of these receptors is not known. Pulmonary mechanoreceptors have not been conclusively demonstrated because previous attempts to distort the pulmonary tissue have also resulted in distortion of other organs in the thoracic and abdominal ca-vity.

Most muscles in birds contain muscle spindles or tendon organs (Dorward, 1970a; Maier, Eldred, 1971; de Wet et al., 1971), but it is not known if af-ferent impulses from these receptors are involved in driving ventilation dur-ing muscle movement.

Although mechanoreceptors are present in the skin and around feathers (Dorward, 1970b), there is no evidence that they are involved in the control

of breathing. Receptors located in the larynx or within the upper respiratory passages can produce apnea when stimulated by water (Jones, Johansen, 1972) or by noxious substances (Eaton et al.,1971). These receptors may have a protective role in preventing material from entering the respiratory tract.

3. <u>Ventilatory responses to neural stimuli</u>. As indicated earlier, during exercise birds overventilate in proportion to the increased rate of metabolism. In recent experiments, we studied the changes in ventilation in ducks that were exercised on a treadmill while holding arterial blood gases nearly constant ($PaCO_2$ increased less than 2 Torr). Ducks were unidirectionally ventilated with a constant flow of gas, thereby uncoupling their respiratory effort from the gas exchange function of the lung. The ventilatory effort in these ducks markedly increased during exercise (400% over rest), with only a small fraction of that increase (5%) accounted for by the slight increase in $PaCO_2$. These data suggest that nonchemical, nonthermal factors are of great importance in the control of breathing, expecially during activity. Use of exercise as an experimental tool may provide insight into the multiple interrelationships of the factors that influence the respiratory controller.

R e f e r e n c e s

Ballam G.O., Kunz A.L., Clanton T.L., Michal E.K. - Fed. Proc., 1981a, 40.
Ballam G.O., Clanton T.L., Kunz A.L. - Physiologist, 1981b, 24, p. 132.
Barnas G.M., Estavillo J.A., Mather F.B., Burger R.E. - Respir. Physiol., 1981, 43, p. 315-325.
Bech C., Nomoto S. - J. exp. Biol.,1982, 97, p. 345-358.
Boon J.K., Kuhlmann W.D., Fedde M.R. - Respir. Physiol., 1980, 39, p. 169-181.
Bouverot P. - Physiol. Rev., 1978, 58, p. 604-655.
Bouverot P., Douguet O., Sébert P. - J. Comp. Physiol., 1979, 133, p. 177-186.
Bouverot P., Hildwein G., Le Goff D. - Respir. Physiol., 1974b, 22, p.137-156.
Bouvsrot P., Leitner L.-M. - Respir. Physiol., 1972, 15, p. 310-320.
Brackenbury J.H., Glesson M., Avery P. - Comp. Biochem. Physiol., 1981, 69A, p. 449-453.
Butler P.J., West N.H., Jones D.R. - J. exp. Biol., 1977, 71, p. 7-26.
Crank W.D., Kuhlmann W.D., Fedde M.R. - Respir. Physiol., 1980, 41, p. 71-85.
De Kock L.L. - Acta anat., 1958, 35, p. 161-178.
De Wet P.D., Farrell P.R., Fedde M.R. - Poultry Sci., 1971, 50, p. 1349-1357.
Dorward P.K. - J. Physiol. (L.), 1970a, 211, p. 1-17.
Dorward P.K. - Comp. Biochem. Physiol., 1970, 35, p. 729-735.
Dreyer M.V., De Boom H.P.A., De Wet P.D. et al. - Acta anat., 1978, 102, p. 217-231.
Dreyer M.V., De Boom H.P.A.,De Wet P.D.et al-Acta anat.,1977,99, p. 192-200.
Duke G.E., Kuhlmann W.D., Fedde M.R. - Poultry Sci., 1977, 56, p. 297-299.
Eaton J.A. Jr., Fedde M.R., Burger R.E. - Respir. Physiol.1971, 11,p.167- 177.

El Hadi H., Sykes A.H. – Brit. Poultry Sci., 1982, 23, p. 49–57.

Estavillo J., Burger R.E. – Am. J. Physiol., 1973, 225, p. 1063–1066.

Fedde M.R. – In: Avian Physiology / Ed. by P.D.Sturkie. 3rd ed. N.Y.: Springer, 1976, p. 122–145.

Fedde M.R., Gatz R.N., Slama H., Scheid P. – Respir. Physiol., 1974a, 22, p. 99–114.

Fedde M.R., Gatz R.N., Slama H., Scheid P. – Respir. Physiol., 1974b, 22, p. 115–121.

Fedde M.R., Kiley J.P., Powell F.L., Scheid P. – Respir. Physiol., 1982, 47, p. 121–140.

Fedde M.R., Peterson D.F. – J. Physiol. (L.), 1970, 209, p. 609–625.

Fedde M.R., Scheid P. – Respir. Physiol., 1976, 26, p. 223–227.

Fedde M.R., Kuhlmann W.D. – In: Respiratory Function in Birds, Adult and Embryonic / Ed. by J.Piiper. N.Y.: Springer, 1978, p. 33–50.

Hodges R.D., King A.S., King D.Z., French E.I. – Cell Tiss. Res., 1975, 162, p. 483–497.

Jones D.R., Johansen K. – In: Avian Biology. Vol. 2 / Eds. D.S.Farner, J.R.King. N.Y.: Academic Press, 1972, p. 157–285.

Kiley J.P., Kuhlmann W.D., Fedde M.R. – J. Appl. Physiol: Respirat. Environ. Exercise. Physiol., 1979, 47, p. 827–833.

King A.S., King D.Z., Hodges R.D., Henry J. – Cell Tiss. Res., 1975, 162, p. 459–473.

Kobayashi S. – Arch.histol. jap., 1969, 31, p. 9–19.

Kobayashi S. – Arch. histol. jap., 1971, 33, p. 397–420.

Linsley J.G., Burger R.E. – Poultry Sci., 1964, 43, p. 291–305.

Mater A., Eldred E. – J. Comp. Neurol., 1971, 143, p. 25–37.

Mather F.B., Barnas G.M.,,Burger R.E. – Comp. Biochem. Physiol., 1980, 67A, p. 265–268.

Milsom W.K., Jones D.R., Gabbott G.R.J. – J. Appl. Physiol.: Respirat. Environ. Exercise Physiol., 1981, 50, p. 1121–1128.

Nye P.C.G., Burger R.E. – Respir. Physiol., 1978, 33, p. 299–322.

Powell F.L., Gratz R.K., Scheid P. – Respir. Physiol.,1978, 35, p. 65–77.

Rautenberg W., May B., Necker R., Rosner G. – In: Respiratory Function in Birds, Adult and Embryonic / Eds. J.Piiper. N.Y.:Springer, 1978, p. 204–210.

Richards S.A. – Biol. Rev., 1970, 45, p. 223–264.

Richards S.A., Avery P. – In: Respiratory Function in Birds, Adult and Embryonic / Eds. J.Piiper. N.Y.: Springer, 1978, p. 196–203.

Scheid P., Gratz R.K., Powell F.L., Fedde M.R. – Respir. Physiol., 1978, 35, p. 361–372.

Scheid P., Slama H., Gatz R.N., Fedde M.R. – Respir. Physiol., 1974, 22, p. 123–136.

Schmidt–Nielsen K., Kanwisher J., Lasiewski R.C. et al. – Condor, 1969, 71, p. 341–352.

Sebert P. – IRCS Medical Science, 1978, 6, p. 444.

Sebert P. – J. Physiol. (P.), 1979, 75, p. 901–909.

Torre–Bueno J.R. – In: Respiratory Function in Birds, Adult and Embryonic / Ed. by J.Piiper. N.Y.: Springer, 1978, p. 89–94.

# RESPIRATORY ADAPTATIONS TO HIGH ALTITUDE IN BIRDS

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## INTRODUCTION

Existence at high altitude presents one of the most rigorous physiologic challenges to living organisms on the surface of the earth. In spite of this, species from all four classes of terrestrial vertebrates do occur at altitudes in excess on 3500 meters. Members of the class Aves have clearly been the most successful of the terrestrial vertebrates at invading the high altitude environment, both in the air and on the ground. The record altitude for any vertebrate was recorded when an aircraft struck a soaring Ruppell's Griffon (Gyps rueppellii) at 11,300 meters and observations of flight at high altitudes have been made on several other species in the Himalayas and North America (Layborne, 1974). How representative of normal flying altitude these records are, however, is uncertain, although at least one species, the Bar-headed Goose (Anser indicus), has been repeatedly observed flying at altitudes up to 9200 meters during its twice-annual migration over the Himalayas (Swan, 1961). In addition, Rahn (1977) has assembled nesting records for 11 bird species at altitudes over 4900 meters, with 5 of these above 5000 meters including the Alpine Chough (Pyrrhocorax graculis) at 6550 meters. An examination of the literature suggests that reptiles occur no higher than 5400 meters (Swan, Leviton, 1962) and mammals exist continuously no higher than 5500 meters (Schaller, 1977).

## HIGH ALTITUDE RESPIRATION AND GAS EXCHANGE

Although a number of bird species clearly function very successfully at high altitude, the physiologic basis for this ability has not been thoroughly investigated. The primary problem for any animal at high altitude is maintaining adequate $O_2$ transport to the tissues in order to sustain aerobic respiration; thus investigations have primarily addressed various aspects of $O_2$ transport under hypoxia. Although numerous studies exist describing responses of the avian respiratory system to hypoxia, they add little insight to the question of existence at extreme altitude, since they either have been performed on unconscious or chemodenervated animals (e.g., Ray, Fedde, 1969; Bouverot et al., 1979) or have failed to expose the birds to hypoxia as severe as that encountered at extreme altitude (Bouverot et al., 1976; Jones, Holton, 1972).

### Tolerance to Extreme Hypoxia

Only three studies have examined birds near their limits of hypoxic tolerance. Tucker (1968) found that Budgerigars (Melopsittacus undulatus) could fly in a hypobaric chamber up to about 3700 meters, while House Sparrows (Passer domesticus) could fly up to 6100 meters and maintained consciousness up to 9140 meters. Colacino et al. (1977) found that Pekin Ducks (Anas platyrhynchos forma domestica) easily tolerated 9000 meters and showed no decrease in their ability to extract $O_2$ from the air up to 6000 meters. Black and Tenney (1980) found that Pekin Ducks and Canada Geese (Branta canaden-

sis) showed none of the behavioral reactions typical of severe cerebral cerebral hypoxia as high as 7600 meteres, while captive-bred Bar-headed Geese showed no reactions below 10,670 meters. After 15 minutes at 12,190 meters, Bar-headed Geese could stand and hold their heads erect. Hypoxic tolerance thus varies among avian taxa, but of the groups examined, waterfowl, especially Bar-headed Geese, are most tolerant.

## Ventilatory Response to Hypoxia

Birds show a pattern of augmented ventilation ($\dot{V}_E$) with both acute and chronic exposure to hypoxia similar to that seen in mammals, although the pattern of change in tidal volume and breathing frequency producing the increased $\dot{V}_E$ differs (Ray, Fedde, 1969; Jones, Purves, 1970). Further, in species which have evolved at high altitude, the increase in $\dot{V}_E$ first appears at much more severe levels of hypoxia than when it first appears in sea-level species. Pekin Ducks show a noticeable increase in $\dot{V}_E$ at $Pa_{O_2} < 50$ torr, while Bar-headed Geese do not show a comparable increase until $Pa_{O_2} < 35$ torr (Black, Tenney, 1980). As in other vertebrates, the hypoxic ventilatory response is mediated by the carotid body, although Van Nice et al. (1980) have suggested that in birds the carotid body may sense arterial $O_2$ content ($Ca_{O_2}$) rather than $Pa_{O_2}$.

## Gas Exchange During Hypoxic Exposure

Once inspired gas has been moved convectively to the vicinity of the exchange surface, $O_2$ movement from the gas phase into blood occurs via diffusion. At this point two factors will profoundly influence $Pa_{O_2}$ and thus the degree of hypoxia which can be tolerated: 1) the absolut $P_{O_2}$ of gas in the vicinity of the exchange surface, and 2) the magnitude of the partial pressure gradient required to move sufficient $O_2$ into the blood to support metabolic demands (a reflection of air-blood diffusion resistance). In the alveolar lung, which is found in all terrestrial vertebrate classes except birds, $P_{A_{O_2}}$ (alveolar $P_{O_2}$) must be less than $P_{I_{O_2}}$ (inspired $P_{O_2}$). Although the increased $\dot{V}_E$ which occurs with hypoxia will raise $P_{A_{O_2}}$ closer to $P_{I_{O_2}}$ in the alveolar lung, the $P_{I_{O_2}}$ to $P_{A_{O_2}}$ gradient will always be relatively large since the alveolar lung acts as a ventilated pool type of gas exchanger (Piiper, Scheid, 1975). The inspired-arterial $P_{O_2}$ gradient present under conditions of extreme hypoxia has been found to be much smaller in birds than in mammals (Table 1) probably due to the more efficient parabronchial lung (Piiper, Scheid, 1975). Even without any other adaptation to high altitude, this ability alone potentially gives birds a great advantage.

The ability of the avian lung to raise $Pa_{O_2}$ to near $P_{I_{O_2}}$ depends not only upon bringing inspired gas into the parabronchi, but upon having minimal resistance to diffusion between the parabronchial lumen and pulmonary blood capillaries. Scheid (1978) has proposed a comprehensive model for gas exchange in the avian lung which suggests that at rest diffusion resistance is indeed minimal, but that during exercise it increases substantially. Thus, the numbers in Table 1 which seem to explain at least in part the bird's superb hypoxic tolerance may not pertain, since under natural conditions, birds are exposed to the most severe levels of hypoxia only during exercise.

T a b l e 1. Inspired ($P_{I_{O_2}}$ BTPS) and arterial($Pa_{O_2}$) oxygen partial pressures for man (Dejours, 1981), Pekin Duck and Bar-headed Goose (Black, Tenney, 1980) at sea level, near summit of Mt. Everest, and near record altitude for bird (Bar-headed Goose only). Values for man were calculated, values for birds were determined after exposure to hypoxic hypoxia for 15 minutes

|  | Man | | Pekin Duck | | Bar-headed Goose | | |
|---|---|---|---|---|---|---|---|
| Altitude (meters) | SL | 8848 | SL | 9150 | SL | 9150 | 11,580 |
| $P_{I_{O_2}}$ (torr) | 149 | 42 | 146 | 37 | 146 | 37 | 23 |
| $Pa_{O_2}$ (torr) | 91 | 22 | 93.5 | 30 | 92.5 | 28.5 | 22 |

Blood $O_2$ Transport During Hypoxia

Although the avian respiratory system functions very effectively under conditions of hypoxia, those species which have evolved at high altitude have adaptive adjustments in the oxygen-carrying characteristics of the blood which further improve hypoxic performance. Only two bird species native to high altitude have been examined, but in both, the Huallata (Chloephaga melanoptera) from the South American Andes (Hall et al., 1936) and the Bar-headed Goose (Black et al., 1978) hemoglobin-$O_2$ affinity is higher than in sea-level waterfowl.

The effect which this adjustment in hemoglobin-$O_2$ affinity has upon $O_2$ transport by the blood is demonstrated in Figure 1, which shows the relat▸
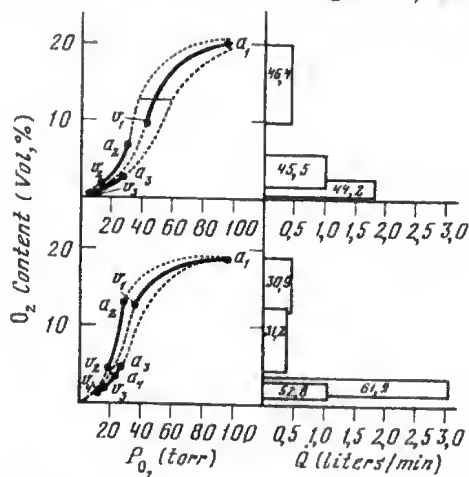


F i g. 1. In vivo  $O_2$ transport in the Pekin Duck (top panels) and Bar-headed Goose (bottom panels) exposed progressively to gas mixture corresponding to sea level and three altitudes. $a_x$ = arterial points, $v_x$ = venous points. Left panels: middle dissociation curves, $a_1$, and $v_1$ – sea level; left dissociation curves, $a_2$ and $v_2$ – 9150 meters; right dissociation curves, $a_3$ and $v_3$ – 10,668 meters; right dissociation curves, $a_4$ and $v_4$ – 11,580 meters (Goose only). Right panels: area in boxes proportional to blood $O_2$ transport (numbers = $\dot{V}_{O_2}$, ml/min); horizontal side, cardiac output; vertical side, a-v $O_2$ content difference. (Data from Black and Tenney, 1980)

ionship between $O_2$ consumption, cardiac output, and $O_2$ delivery to tissue capillaries by the blood (arterial-venous $O_2$ content difference x cardiac output) for Pekin Ducks and Bar-headed geese at $P_{IO_2}$ levels simulating sea level, 9150 meters (near summit for Mt. Everest), 10,668 meters, and 11,500 meters (near record altitude for a bird). Sea-level arterial and venous points ($a_1$ and $v_1$) show that the resting Pekin Duck is operating on the upper half of the dissociation curve, while the goose is using only the more shallow upper third. In spite of this and the fact that when compared to the duck, the goose has a smaller a-v $O_2$ content difference, lower oxygen consumption, and a similar cardiac output, it still has a much lower mixed venous $P_{O_2}$. This is primarily due to the Goose's higher hemoglobin-oxygen affinity.

Exposure of both species to hypoxia simulating 9150 meters results in the in vivo dissociation curve shifting to the left. Arterial and venous points ($a_2$ and $v_2$) show that here the goose is operating on the steepest portion of the dissociation curve, while the duck is operating on the much more shallow, lower end of the curve. At this point the goose has a higher mixed venous $P_{O_2}$ (18 torr vs 13.5 torr) than the duck, a lower minute ventilation (Black, Tenney, 1980), lower oxygen consumption, and a lower cardiac output, indicating that it is able to maintain relatively good oxygen transport to the tissues at this altitude while still having reserve capacity for exercise. The less than normoxic cardiac output level suggests that the increased oxygen demands imposed by exercise can potentially be met without significantly lowering mixed venous $P_{O_2}$. This is of course critical since the only point at which the bar-headed goose will encounter such extreme hypoxia is during flight. Although the metabolic cost of high-altitude flight is unkown, it is unlikely to be any less than the 9-10 times standard metabolic rate determined for a variety of species flown in wind tunnels under sea-level conditions (Hart, Berger, 1972).

Increased $CO_2$ production by muscle during exercise also could potentially raise oxygen transport efficiency. Under the resting conditions employed in this study, arterial and mixed venous pH were nearly the same at all simulated altitude levels and both venous and arterial $P_{CO_2}$ were very low (Black, Tenney, 1980); thus, the full potential impact of the Bohr effect cannot be seen. During strenuous exercise higher venous $P_{CO_2}$ levels due to increased metabolism would presumably result in considerably greater a-v pH differences, making the in vivo dissociation curve even steeper than the one plotted. Assuming the same arterial point, a steeper dissociation curve would allow a greater a-v oxygen content difference and therefore increased $O_2$ delivery to the tissue for the same mixed venous $P_{O_2}$.

At simulated altitudes of 10,668 and 11,580 meters, the dissociation curve is shifted to the right for both species, presumably due to metabolic acidemia (Black, Tenney, 1980). Arterial and venous points drop from the steep portion of the curve down onto the shallow, lower end, and a-v oxygen content difference decreases drastically. This necessitates an increase in cardiac output, eliminating the reserve capacity needed to sustain exercise and causes a decrease in mixed venous $P_{O_2}$ to very low levels, eliminating the partial pressure gradient required to move oxygen from capillaries to tissue

cells. Thus, it is unlikely that the Bar-headed Goose could sustain flight much above the 9100 meter level; this is sufficient however to enable these birds to cross the highest barriers on their migratory path. Thus, there appears to have been selection for birds possessing hemoglobin-$O_2$ affinity which enable them to fly up to about 900 meters (see Swan, 1970 for discussion of evolutionary history of this species).

One additional physiologic response to hypoxia which could potentially improve hypoxic performance has been described. Grubb et al. (1978, 1979) found that Pekin Ducks increase cerebral blood flow by as much as six-fold when exposed to hypoxia simulating an altitude of 9000 meters. These studies did not measure cardiac output, however. Thus, it is not clear whether the six-fold increase represents an actual increase in the portion of cardiac output going to the brain. Figure 1 show that in response to hypoxia Pekin Ducks increase their cardiac output by at least four-fold while Bar-headed Geese are capable of slightly more than a six-fold increase. Thus, the increase in cerebral blood flow measured by Grubb et al. may only be reflecting an increase in cardiac output.

Finally, Figure 1 emphasizes that under the hypoxic conditions likely to be encountered by Bar-headed Geese on migration, sustained performance requires $O_2$ transport sufficient to maintain aerobic respiration. Hemoglobin-$O_2$ affinity in the Bar-headed goose is such that $O_2$ transport by the blood at a simulated altitude of 9150 meters is most efficient only when arterial pH is relatively alkalotic. The avian lung is probably capable of maintaining a relatively low $P_{CO_2}$ even under conditions of maximal exercise, but if the acid by-products of anerobic respiration accumulate in the blood, the in vivo dissociation curve will shift to the right as is seen when the birds are exposed to the most severe hypoxic levels. When this occurs $Ca_{O_2}$ falls to levels incompatible with sustaining adequate $O_2$ transport.

### SUMMARY

Birds are more tolerant of extreme hypoxia than any other class of terrestrial vertebrates; they have been found flying as high as 11,300 meters. Although birds show the same pattern of augmented ventilation in response to hypoxia that is seen in mammals, they are capable of reducing the inspired to arterial $P_{O_2}$ gradient to only a few torr when exposed to extreme hypoxia. Native high-altitude species (e.g., Bar-headed Goose) have a genetically-based increase in hemoglobin-$O_2$ affinity when compared to sea-level species. Bar-headed Geese can maintain $O_2$ transport under resting conditions without an increase in cardiac output up to a simulated altitude of 9150 meters, suggesting that adequate reserve to support flight metabolism is present. However, adequate $O_2$ transport during exercise can be maintained only under conditions of aerobic respiration and relative arterial alkalosis.

### ACKNOWLEDGMENTS

R e f e r e n c e s

Black C.P., Tenney S.M. - Respir. Physiol., 1980, 39, p. 217-239.
Black C.P., Tenney S.M., Van Kroonenburgh M. - In: Respiratory Function in
    Birds, Adult and Embryonic / Ed. by J.Piiper. B.: Springer-Verlag, 1978,
    p. 79-83.
Bouverot P., Douguet D., Sebert P. - J. Comp. Physiol., 1979, 133, p. 177-
    186.
Bouverot P., Hildwein G., Oulhen P.H. - Respir. Physiol., 1976, 28, p. 371-
    385.
Dejours P. Principles of Comparative Respiratory Physiology Second Revised
    Ed. Elsevier/North-Holland, Inc., 1981.
Colacino J.M., Hector D.H., Schmidt-Nielsen K. - Respir. Physiol., 1977, 29,
    p. 265-281.
Grubb B., Colacino J.M., Schmidt-Nielson K. - Am. J. Physiol., 1978, 234(3),
    p. H230-H234.
Grubb B., Jones J., Schmidt-Nielson K. - Am. J. Physiol., 1979, 236(5),
    p. H744-H749.
Hall J.G., Dill D.B., Guzman Barron E.S. - J. Comp. Cell. Physiol., 1936,
    8(3), p. 301-313.
Hart J.S., Berger M. - In: Proc. XV Intern. Ornithol. Congr. Hague, 1972,
    p. 189-199.
Jones D.R., Holeton G.F. - J. Exp. Biol., 1972, 56, p. 657-666.
Jones D.R., Purves M.J. -J. Physiol.,1970, 211, p. 295-309.
Laybourne R.C. - Wilson Bull., 1974, 86, p. 461-462.
Piiper J., Scheid P. - Respir. Physiol., 1975, 23, p. 209-221.
Rahn H. - In: Respiratory Adaptations, Capillary Exchange and Reflex Me-
    chanisms, Proc. of Krogh Centenary Symposium. Srinagar, India / Eds.
    A.S.Paintal and P.Gill-Kumar., 1977, p. 94-105.
Ray P.J., Fedde M.R. - Respir. Physiol., 1969, 6, p. 135-143.
Schaller B. Mountain Monarchs - Wild Sheep and Goats of the Himalyayas.
    University of Chicago Press, 1977.
Scheid P. - Respir. Physiol., 1978, 32, p. 27-49.
Swan L.W. - Sci. Am., 1961, 205, p. 68-78.
Swan L.W. - Nat. Hist., 1970, 79, p. 68-75.
Swan L., Leviton A. - Proc. Calif. Acad. Sci., 1962, 32, p. 103-147.
Tucker V.A. - J. Exp. Biol., 1968, 48, p. 55-66.
Van Nice P., Black C.P., Tenney S.M. - Comp. Biochem. Physiol., 1980, 66A,
    p. 347-350.

PHYSIOLOGY AND METABOLISM IN BREATH-HOLD DIVING

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INTRODUCTION

Diving birds can be forced to remain submerged for periods of time which would kill their more strictly terrestrial relatives. The single physiological variable most often recorded as an indicator of this capacity for underwater endurance is the heart rate. However, in a single species, Anas platyrhynchos, heart rate data have been amplified by recording blood pressures (Butler, Jones,1971), cardiac output and its distribution (Folkow et al., 1967; Jones et al., 1979) and even redox balance of cerebral tissues (Bryan, Jones,1980a,b). Nevertheless, even if only heart rate is recorded, it now seems possible to identify three different types of diving response depending on whether the animal is diving voluntarily or is forcibly submerged.

TYPES OF DIVING RESPONSE

1. Forced dive response: exemplified by laboratory studies, in which the head of an animal is submerged in a beaker of water. Heart rate falls more rapidly in diving than dabbling ducks but after 40 s or so of the dive it stabilises at a rate which may be one-tenth of the pre-dive value. Heart rate stays at this level for several minutes and then it usually doubles, but it is still only one-fifth the surface value, remaining at this level for the rest of the dive.

The fall in heart rate is taken to indicate a like decline in cardiac output which is offset by a sufficient increase in total peripheral resistance to keep mean arterial blood pressure constant. Most tissues don't receive any measurable vascular supply while others, such as the heart and brain, have their blood supply maintained or increased (Jones et al.,1979). Consequently, we assume that oxygen, stored in the body at the start of the dive, is saved for the heart and brain while the other tissues metabolise anaerobically. At the end of the dive, cardiac output increases dramatically and flow is restored to all regions of the body. Products of anaerobic metabolism are flushed from the tissues and minute ventilation is elevated for a period which varies directly with the duration of the preceding dive (Lillo, Jones, 1982).

2. Conditioned dives: these are short forced dives (40 s duration), which are performed repetitively during several days until the animal no longer displays a fall in heart rate. At the start of a series of trials, heart rate in naive ducks falls to about 20% of the pre-dive value in 40 s of diving. Repeating the diving protocol, over several days, results in less and less heart rate change during a dive until, in fully conditioned animals, heart rate remains at the surface rate throughout the dive. Since there appear to be no cardiovascular adjustments in the conditioned animals it seems reasonable to assume that metabolism remains at the surface level yet, surprisingly, arterial oxygen tension after 35-40 s submergence is the same in naive as in conditioned ducks. Giving naive ducks 100% oxygen to breath pre-dive prevents bradycardia, while if conditioned ducks are pre-treated with slightly reduced oxygen (15% $O_2$ in $N_2$) bradycardia always develops in the 40 s dive.

990

The period of hyperventilation at the end of conditioned dive is short and there is no post-dive tachycardia.

3. Voluntary dives: these are short dives (10-40 s) in which the animal is swimming actively. It is presumed that metabolism is elevated in these dives by 3.5 to 4 times the resting level (Prange, Schmidt-Nielsen, 1970; Woakes, Butler, 1982). Nevertheless cardiovascular adjustments are made which are quite distinct from those which are associated with exercise on land. Just before a dive, ducks hyperventilate and heart rate increases. On submergence heart rate falls rapidly to its lowest value and then increases attaining a steady level after 6-8 s (Butler, Woakes, 1979). This steady heart rate is above the resting level in pochards (Aythya ferina), tufted ducks (A.fuligula), cormorants (Phalacrocorax auritus) and penguins (Pygoscelis adeliae) and may even be as high as when the animals are swimming on the surface at the same speed (Millard et al., 1973; Butler, Woakes, 1979; Kanwisher et al., 1981; Butler, 1982). Frightening ducks to dive results in higher underwater heart rates. Preventing tufted ducks from surfacing after voluntary dives causes a marked fall in heart rate. Only a brief recovery period follows each dive before the animal is again ready for the next underwater excursion. Dives usually occur in a seriss and heart rate remains around three times the resting rate in the periods between dives.

MAXIMUM DIVE TIMES IN FORCED, CONDITIONED AND
VOLUNTARY DIVES

The maximum dive time that can be endured depends on the amount of oxygen stored in the body at the start of the dive, the capability for mobilization of this oxygen store, and the rate at which oxygen is utilised by the tissues. In a forced dive, blood supply is preferentially directed to the central nervous system and heart although, as the circulation is divided, blood also flows through the lungs. Assuming that only these three tissues will be draining the oxygen reservoir in the dive then, if the size of the oxygen store is known, by estimating the oxygen consumption by these tissues we obtain a value for maximum underwater endurance. The amount of oxygen stored in blood and lungs at the start (that in other body tissues is not available for the heart, lung or brain), and that remaining at the end of a maximum dive has been measured. For a 1 kg domestic duck (Anas platyrhynchos) the amount of oxygen used from ths store is 20.76 ml (Hudson, Jones, 1983). In a 1 kg duck the brain weighs 5 g (Hudson, Jones,1983) and the spinal cord about half this. The weight specific metabolic rate of the cord is about half that of the brain (Mink et al., 1981). Using figures for brain metabolic rate, estimated for chicken by Mink st al., 1981 (about 0.06 $ml \cdot g^{-1} \cdot min^{-1}$), then the brain and spinal cord use oxygen at a rate of 0.5 $ml \cdot min^{-1}$. The lung mass of a 1 kg duck is about 12 g (Lasiewski, Calder, 1971) and metabolic rate of mammalian lungs is anywhere from 0.004 to 0.02 $ml \cdot g^{-1} \cdot min^{-1}$ (Krebs, 1950; Wallace et al.,1974). Henoe the lungs could use from 0.05 to 0.24 $ml \cdot min^{-1}$. Howevsr, since brachial blood supply is greatly reduced in a forced dive (Jones et al., 1979) then perhaps we should take the lower value. Cardiac oxygen consumption can be calculated from the external work done by the right and left ventricles if the efficiency of cardiac contraction is known (Jones, Johansen, 1972). The extsrnal work done is the product of

cardiac output and arterial blood pressure. The rather complex relation between heart rate and dive time must be taken into account but if stroke volume remains fixed at 1.5 ml then the heart will use, on average, 0.9 ml·min$^{-1}$ if it works at 10% efficiency. Hence the total oxygen utilisation rate is 1.45 ml·min$^{-1}$ and maximum dive time will be 14.2 minutes. This compares well with experimentally derived values for two ducks of 1.3 kg mass which dived for 9 and 11.0 minutes (Hudson, Jones, 1983), particularly in view of the fact that we have not taken account of the oxygen demand of tissues such as the eyes and adrenals in this calculation.

For conditioned dives the calculation is greatly simplified. Since there are no cardiovascular changes then it seems reasonable to suggest that metabolic changes from rest are unlikely. What then is the resting metabolic rate likely to be under laboratory conditions? Calculations from the relationship between body weight and metabolic rate predict a resting oxygen uptake for a 1 kg duck of 11.3 ml·min$^{-1}$ (Lasiewski, Dawson, 1967). However, our own and data of others suggest that, in the laboratory, resting metabolic rate is at least twice this value (Prange, Schmidt-Nielsen, 1970; Jones, Holeton, 1972) so, if the maximum available store of oxygen is 20.76 ml then it will last for 55 s, which is slightly longer than we are usually able to condition ducks to maintain their heart rates at resting levels.

What sort of metabolic profile should we assume for a voluntary dive? It is possible to measure the speed at which the animal swims underwater and relate this to what its oxygen consumption is when it is swimming at the same velocity on the surface (Woakes, Butler, 1982). Nevertheless, the fact that some cardiovascular changes occur implies that there may be some preferential redistribution of blood flow (i.e. to active muscles). Woakes and Butler (1982) report the oxygen usage in voluntary dives is approximately 3.5 times resting which, for a 1 kg tufted duck (A.fuligula), is about 32.5 ml·min$^{-1}$. At this rate of oxygen utilisation then the duck could dive, without recourse to anaerobic metabolism, for 38 s if its oxygen store was no bigger than that in the domestic duck (A.platyrhynchos). The longest reported natural dive in this species is about 40 s (Dewar, 1924).

RELATION BETWEEN BODY MASS AND DIVE TIME

Given that the animals in conditioned or voluntary dives have the same ability to withdraw oxygen from the store as in forced dives then it is possible for both these dives to be made without recourse to anaerobic energy production. However, aerobic diving places definitive limits on the animal's underwater abilities. These abilities can be stretched by using combinations of aerobic and anaerobic diving or by increasing the size of the oxygen store. Since the size of the oxygen store increases slightly more proportionately than body mass increases, while metabolism increases somewhat less, then one might predict a selection pressure for large body size in diving birds.

If we assume that in conditioned or voluntary dives there are no circulatory adaptations which will affect the relation between metabolic rate and mass (Lawiewski, Dawson, 1967) then for these dives

Metabolism $\propto$ Mass$^{0.723}$

However, the relation between the size of the oxygen store and body mass (Hudson, Jones, 1983), expressed in the allometric form, is

Oxygen Store $\propto$ Mass$^{1.131}$

Therefore in aerobic diving, maximum underwater endurance (dive time) is related to mass as follows

$$\text{Maximum aerobic dive time} \propto \frac{\text{Mass}^{1.131}}{\text{Mass}^{0.723}}, \quad \propto \text{Mass}^{0.4}.$$

Consequently, if mass increases by 10 times then maximum aerobic dive time will only go up about 2.5 times.

In forced dives, on the other hand, most of the oxygen is used by the heart and brain. In ducks the size of the heart increases in almost strict proportion to body mass while the relation for the brain is much less. The combined relation for the heart and brain is

Heart and Brain Mas $\propto$ Mass$^{0.65}$

However, the actual rate of metabolism of heart and brain will not increase in strict proportion to their increase in mass but rather to mass raised to the 0.73 power. Hence, in forced diving, maximum underwater survival should be related to mass in the following manner

$$\text{Maximum forced dive time} \propto \frac{\text{Mass}^{1.131}}{(\text{Mass}^{0.65})^{0.73}}, \quad \propto \text{Mass}^{0.65}.$$

Therefore size confers a greater advantage on survival in forced rather than aerobic dives, for if body mass increases 10 times then underwater endurance will go up nearly 5 times in forced dives. In fact, we have established experimentally that for forced dives the relation between body mass and dive time is $\propto$ Mass$^{0.64}$.

CONCLUSIONS

Aerobic limits set maximum dive times in forced, conditioned and voluntary dives but, in forced dives, the limit is set by the metabolic rate of only two tissues (heart and central nervous system) whereas, in conditioned and voluntary dives, the total aerobic metabolism probably sets the limit. Whether diving birds exercise the full range of options which appear to be open to them for natural diving is unknown. Obviously, the oxygen sparing, forced dive response will be useless to an animal which has used up all its oxygen stores in an aerobic dive. The forced dive response can only be of value when it is effected while much of the oxygen store remains unused. In other words, a reserve of oxygen must be kept on hand in both conditioned and voluntary dives. This appears to be the case, for bradycardia rapidly ensues in conditioned ducks after 40 s submergence which is about two-thirds of their calculated maximum aerobic tolerance. Furthermore, most voluntary dives are very short, about 10-20 s (Butler, Woakes, 1979), which is only half the calculated maximum aerobic tolerance.

Aerobic diving confers advantages on the animal in terms of the total amount of time that can be spent underwater in a given time period. Recovery from forced dives is a long process and the length of time required for complete recovery varies directly with the length of the dive (Lillo, Jones, 1982; Butler, Jones, 1982). Recovery from diving may have two components with very different time courses, one, a short time course component representing

replenishment of the body oxygen stores and two, a long time course component representing breakdown or elimination of the products of anaerobic metabolism. After aerobic diving only the first component is observed. Thus, in a one-hour diving period, the animal could opt for a strategy of one maximal dive of 10 minutes duration which would require at least 50 minutes for recovery (Butler, Jones, 1982) or a series of 30 s dives with about 20 s for recovery from each dive. The latter strategy allows the duck to be underwater for 36 min of the one-hour period.

On the other hand, any disadvantages of diving aerobically for short periods have not been clarified. The major constraint on this kind of activity is that the animal must be equipped with a mechanism which either causes it to surface or go into the forced dive response before its oxygen stores are exhausted. Certainly, there seems to be no advantage to the forced dive response in short dives, even in terms of oxygen conservation. In naive and conditioned ducks the same amount of oxygen is removed from the blood in the first 40 s of the dive despite bradycardia in naive ducks.

R e f e r e n c e s

Bryan R.M., Jones D.R. - J. Physiol., 1980a, 299, p. 323-336.
Bryan R.M., Jones D.R. - Am. J. Physiol., 1980b, 239, p. R352-R357.
Butler P.J., Jones D.R. - J. Physiol., 1971, 214, p. 457-479.
Butler P.J., Jones D.R. - In: Advances in Physiology and Biochemistry.
    Vol. 8 / Eds. by O.E.Lowenstein. N.Y.: Academic Press, 1982.
Butler P.J., Woakes A.J. - J. exp. Biol., 1979, 79, p. 283-300.
Dewar J.M. The Bird as a Diver. L.: H.F. and G.Witherby, 1924.
Folkow B., Nilsson N.J., Yonce L.R. - Acta physiol. scand., 1967, 70,
    p. 347-361.
Jones D.R., Bryan R.M., West N.H. et al. - Can. J. Zool., 1979, 57,p.995-1002.
Jones D.R., Holeton G.F. - J. Exp. Biol., 1972, 56, p. 657-666.
Jones D.R., Johansen K. - In: Avian Biology / Ed. by D.J.Farner,J.R.King.
    N.Y.: Academic Press, 1972, p. 157-285.
Kanwisher J.W., Gabrielsen G., Kanwisher N. - Science, 1981, 211, p. 717-719.
Krebs M.A. - Biochem. Biophys. Acta, 1950, 4, p. 249-269.
Lasiewski R.C., Calder W.A. - Resp. Physiol., 1971, 11, p. 152-166.
Lasiewski R.C., Dawson W.R. - Condor, 1967, 69, p. 13-23.
Lillo R.S., Jones D.R. - J. appl. Physiol., 1982, 52, p. 206-215.
Millard R.W., Johansen K., Milsom W.K. - Comp. Biochem. Physiol., 1973,
    46A, p. 227-260.
Mink J.W., Blumenschine R.J., Adams D.B. - Am. J. Physiol., 1981, 241,
    p. R203-R212.
Prange H.D., Schmidt-Nielsen K. - J. exp. Biol., 1970, 53, p. 763-777.
Wallace H.W., Stein T.P., Liquori E.M. - J. Thor. Cardiovasc. Surg., 1974,
    68, p. 810-814.

# NEW TECHNIQUES FOR STUDYING RESPIRATION IN FREE FLYING BIRDS

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## INTRODUCTION

Bartholomew (1974) stated "if one excludes the ratites and penguins, everything birds do is in one way or another linked to flight". In addition to this, some of the achievements of birds during migratory flight are quite remarkable. Non stop flights of 2,700 km for the lesser snow goose, Anser c. caerulescens (Ogilvie, 1978) and of 3,800 km for the Pacific golden plover, Pluvialis dominica fluva, (Johnston, McFarlane, 1967) have been reported, while a flock of bar headed geese (A.indicus) was observed flying over the summit of Mt Everest (Swan, 1961); an altitude of approximately 9,000 m. At this altitude, environmental oxygen tension is 52 mmHg and maximum oxygen uptake in man is close to his basal oxygen requirements. It is not surprising, therefore, that ornithologists have been fascinated by various aspects of bird flight, particularly navigation and energy requirements of migration. It is doubtful if any one experimental technique would adequately give all of the necessary data for a full analysis of the energetics and metabolic requirements of flight. This would entail not only measurements of oxygen consumption and various other respiratory and cardiovascular variables but also details of the behaviour of the bird and of the prevailing meteorological conditions. It would be necessary to know the strength and direction of the wind etc. (Pennycuick, 1969).

Techniques which allow determinations of metabolism during migration are indirect and details of the birds' flight behaviour have to be assumed. Techniques that allow the direct measurement of oxygen uptake and of other respiratory variables can be used under controlled conditions, but long flights, more closely resembling the conditions of natural migration, are not possible. The recent use of radiotelemetry in imprinted geese may overcome some of these problems.

## MEASUREMENT OF METABOLISM DURING MIGRATION
### a) Weight loss

Some of the earliest values of metabolic rate during flight were estimated from the loss of weight recorded during a long flight with the assumption that fat constitutes by far the major part of this weight loss (Nisbet et al., 1963). Using the calorific value of fat (9.5 kcal $g^{-1}$), these authors calculated that a 19 g blackpoll warbler, Dendroica striata, flying at 6-12°C has a power consumption of approximately 1 kcal $h^{-1}$ (1.16 Wor. 3.5 ml $O_2$ $min^{-1}$) which is 40% of that predicted by allometric formulae based on more recent data (Butler, 1981, 1982). Berger and Hart (1974) have criticised the method of measuring weight loss to determine power input as they believe that weight loss may exceed the production of metabolic water.

### b) $CO_2$ production using doubly labelled water

The central factor of this method is that the oxygen in respiratory $CO_2$

is in isotopic equilibrium with the oxygen in body water (Lifson et al., 1949). Thus, the hydrogen of body water is lost primarily as water whereas the oxygen is lost both as water and as $CO_2$. The turnover rate for the oxygen in body water is greater than that for the hydrogen and the difference is proportional to the $CO_2$ produced. The two turnover rates can be obtained by labelling the two components of body water with stable isotopes of hydrogen and water, viz deuterium and $^{18}O$. Validation of this method by comparing the calculated $CO_2$ production with that measured directly from birds in a respirometer shows that there is an average overestimation of 3-4% for pigeons, Columba livia, (LeFebvre, 1964) and house martins, Delichon urbica, (Hails, 1979). In the former study the mean percentage error was 8%. Although there are certain assumptions associated with this method (lifson, McClintock, 1966), errors in field measurements fo $CO_2$ production can be reduced to 10% (Nagy, 1980). The use of this method by LeFebvre (1964) with pigeons flying a distance of at least 480 km, demonstrated that the value of power imput obtained (22 kcal $h^{-1}$) is similar to that calculated from estimated fat loss (i.e. the difference between estimated fat content at the beginning of flight, based on measurements from other birds, and actual fat content at the end of the flight). It also happens to be within 2% of the value calculated for similar sized birds using the allometric formulae of Butler (1981, 1982). Thus measurement of fat loss and $CO_2$ production using the $D_2O^{18}$ method seem to give reasonable values of power input during long flights, and the technique has been used more recently on smaller birds (Utter, LeFebvre, 1970; Hails, 1979). Actual measurements of oxygen uptake and respiratory performance require more direct recording techniques.

DIRECT MEASUREMENTS USING WIND TUNNELS

The first direct measurement of oxygen uptake of a bird during forward flapping flight was that of Tucker (1966) working with and budgerigars, Melopsittacus undulatus, flying in a closed wind tunnel. The birds had to be trained to fly in the tunnel. Oxygen content of the air in the wind tunnel was measured continuously as a bird flew with no leads or cannulae attached to it. In subsequent papers, Tucker attached a loose fitting mask to the face of budgerigars (Tucker, 1968) and laughing gulls, Larus atricilla (Tucker, 1972). Air was drawn through the mask at a known rate and oxygen measured in the effluent gas (see Fig. 1). These historic papers heralded the beginning of an era when respiratory variables could be recorded from birds flying at controlled velocities and angles. However, only a handful of publications have been forthcoming and a number of them have merely repeated Tucker's measurements on other species (Bernstein et al., 1973; Torre Bueno, Larochelle, 1978). The word "merely" is not meant in any derogatory sense; the author is only too well aware of the difficulties involved in training birds to fly in a wind tunnel. It was possible to get only 5 out of 12 pigeons to fly under such conditions, but we did succeed in obtaining samples of arterial and venous blood during the flights for measurement of blood gases and lactate (Butler et al., 1977).

Only Bernstein and his coworkers have managed to record tidal volume ($V_T$) as well as respiratory frequency and oxygen uptake from birds flying in a wind tunnel. A small, hard wired, air flow transducer (hot-thermistor or hot-

F i g. 1. A pigeon flying in a wind tunnel while wearing a loose fitting mask for measuring $O_2$ uptake and $CO_2$ production. Note the sample tube and thermocouple lead from the mask positioned above the head and along the back of the bird (Butler et al., 1977)

film anemometer) was attached to the mouth of the bird. Below an ambient temperature ($T_A$) of 22°C, $V_T$ almost doubles during flight in the fish crow, Corvus ossifragus, and is independent of flight velocity (Bernstein, 1976), whereas in the white-necked raven, C.cryptoleucus $V_T$ is similar to the resting value during flight (Hudson, Bernstein, 1981). Above $T_A$ 22°C, body temperature ($T_B$) increases during flight in the white necked raven, and in both species, $V_T$ increases as $T_A$ rises. At the lower ambient temperatures, there are similar increases in ventilation volume ($\dot{V}_I$) and oxygen uptake, ($\dot{V}_{O_2}$) above the resting levels, during flight in the fish crow, but above $T_A$ 22°C, the rise in $\dot{V}_I$ is not accompanied by an increase in $\dot{V}_{O_2}$, so oxygen extraction decreases (Bernstein, 1976). Even at lower ambient temperatures, there appears to be a slight increase in effective ventilation, at least in starlings, Sturnus vulgaris, as $P_{O_2}$ in the air sacs increases and $P_{CO_2}$ decreases (Torre-Bueno, 1978a). The extra increase in ventilation during flight at high ambient temperatures would tend to cause further hypocapnia and alkalosis. It has been demonstrated, however, that the white-necked raven resorts to so called "compound ventilation" when flying at high ambient temperatures. This occurs when $T_B$ rises above 43°C. A high frequency, shallow ventilatory component is superimposed upon a deeper, lower frequency component, and may serve to reduce hypocapnia during thermal panting (Hudson, Bernstein, 1978). It has been suggested that during long flights (e.g. migration)birds fly at an altitude where $T_A$ is low enough to prevent hyperthermia and excessive respiratory water loss (Torre-Bueno, 1978b; Hudson, Bernstein, 1981).

Thus, wind tunnels have given us a glimpse of the respiratory adjustments made by birds during flight. However, the technique does have its problems, some of which were outlined by Rothe and Nachtigall (1980) at the XVII International Ornithological Congress. The bird has to fly in a restricted space, must tolerate the noise of the fan motor and is in an optically motionless
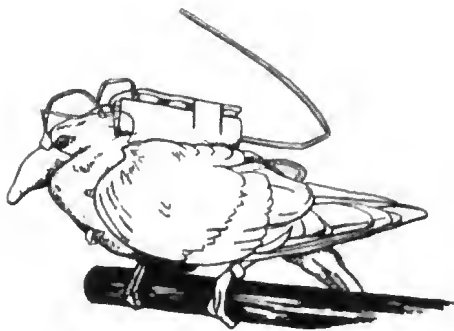
F i g. 2. Pigeon with transmitter and mask for telemetry of respiration rate
and heart rate. Leads from thermistor in the mask and from the ECG electrode
enter front end of transmitter. Power supply is by three Nicad batteries
shown above transmitter. Antenna is shown projecting from back end of unit
(Drawn from photograph in Hart and Roy, 1966, by permission of the publisher
University of Chicago Press)

and monotonous environment. In addition, it may also have to carry an exter-
nally fitting face mask and trailing wires and cannulae, all of which will
affect its flight performance. No doubt related to some of these factors is
the observation that the flight pattern of a pigeon is different in a wind
tunnel than it is during free flight (Butler et al., 1977). Depsite the prob-
lems, Rothe and Nachtigall (1980) could see no alternative to the wind tun-
nel method for the investigation of the physiology of bird flight.

DIRECT MEASUREMENTS USING RADIOTELEMETRY

As a possible alternative to the wind tunnel, radiotelemetry and had not
shown much promise in its early usage. Hart and Roy (1966) published the
first comprehensive set of respiratory data from flying birds (pigeons) using
radiotelemetry. Everything, i.e. face-mask and transmitter, was mounted ex-
ternally (Fig. 2) which must have affected the energy requirements of flight
(Hart, Roy, 1966). To prevent loss of the transmitter, and presumably to
keep the receiver within range of the transmitter, the birds were restrained
by a nylon line tied to the harness, so that the flights were, on average,
of only 9 s duration. Thus, the birds had barely taken off and were nowhere
near a steady state, so that all the measured values were considerably higher
than they would have been after several minutes of flight. Similar criticisms
can be levelled at subsequent papers by these authors (Berger et al., 1970a,
b). A long range (80 km) transmitter was attached externally to herring
gulls and used to monitor heart rate during flights of up to 20 km in distan-
ce (Kanwisher et al., 1978). This is clearly a great advance over the earlier
systems as far as the duration of the flights is concerned, but the external
mounting and the possible lack of information on the bird's behaviour during
such long flights are still defects of the technique.

Although not measuring any respiratory variables, Torre-Bueno (1976) com-
bined the use of radiotelemetry and a wind tunnel. He implanted a small tem-
perature sensing transmitter into starlings and was able to record core and
skin temperature during flights of 0.5-2 h duration. Thus during this work,
998

F i g. 3. Imprinted barnacle geese chicks being taken for a walk by their foster parent (Woakes, 1980)

the bird was not burdened by any externally mounted hardware or leads, the transmitter was maintained close to the receiver throughout the flight and the flight conditions were known at all times. Unfortunately the disadvantages of the wind tunnel (Rothe, Nachtigall, 1980) still remained. It has recently been demonstrated however, that implantable, short range transmitters can be used with freely flying birds engaged in long flights (Butler,Woakes, 1980).

Barnacle geese, Branta leucopsis, were raised from eggs hatched in a laboratory incubator and they were imprinted (Lorenz, 1970) on a human, who gave them as much attention as possible during the first week after hatching. They were kept with this foster parent for 16 h per day during the first week after hatching, and for several hours of that period they were handled. For the next six weeks they were kept indoors and close to the foster parent for 8-9 h per day. During this period they were taken for walks for approximately 1 h every day (Fig. 3) in order to reinforce the "following" response (Brown, 1975) and the foster parent frequently called "come on". At seven weeks they were left outside all day in an open-topped compound which contains two pools. They were still taken for 1 h walks each day and were kept indoors at night. The geese became flighted at 10 weeks of age and were encouraged to fly by the foster parent who ran along the University's athletics track while calling "come on" to the birds. Six geese reached this stage, but 3 were lost during their early exploratory flights before they became accustomed to the local geography. The remaining 3 became proficient flyers and flew around the University campus as they desired, using the compound and pools as a home base. When they were 4 months old, these three geese were taken to a disused airfield where their willingness was tested to fly behind a pick-up truck containing their foster parent.
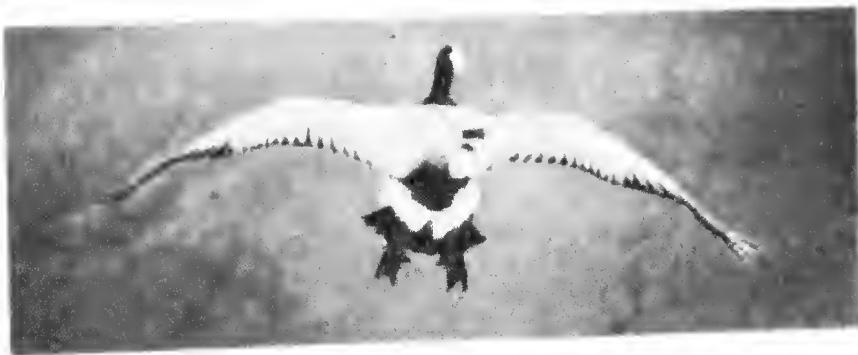
F i g. 4. (a) Barnacle goose flying beside truck containing its foster parent and companions (b) Barnacle goose slope-soaring on the airstream rising over the front of the cab of the truck

One bird at a time was free, the others were caged in the back of the open-topped pick-up truck, and they, together with the foster parent who was also in the truck, were fully visible to the free bird. This goose was placed on the ground and as the truck accelerated away, the bird flew after its foster parent and companions. At the first attempt, two of the geese followed the truck around the airfield (Fig. 4) and allowed themselves to be caught at the end of the flight. The other bird began to follow the truck but soon flew too far away and lost contact with the foster parent; it was never recovered. A two channel, FM radio transmitter (Fig. 5; Woakes, Butler, 1975) was completely implanted into these geese and measurements of heart rate and respiratory frequency were obtained during flights of an average duration of 14.4 min and at a mean air velocity of 18.7 m s$^{-1}$ (Butler, 1980; Butler, Woakes, 1980). A perfectly clean e.c.g. signal was obtained (Fig.6) and by taking a cine film of the geese during flight, respiratory activity (i.e. lung ventilation) could be related to wing beating.

Several interesting features emerged from this preliminary study. Resting values of heart rate and respiratory frequency were approximately 50% lower than the values predicted from allometric formulae. This could have been
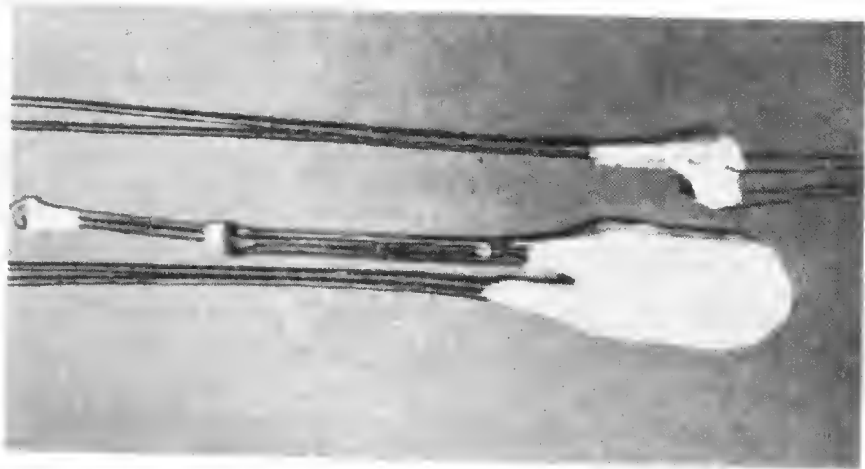
F i g. 5. Encapsulated, two channel FM radiotransmitter used for transmitting respiratory frequency and heart rate from free flying barnacle geese. The bipolar ECG electrode was placed next to the heart underneath the sternum, the transmitter was placed in the abdominal cavity and the thermistor was placed in the lumen of the trachea. The leads between the thermistor and transmitter were run under the skin
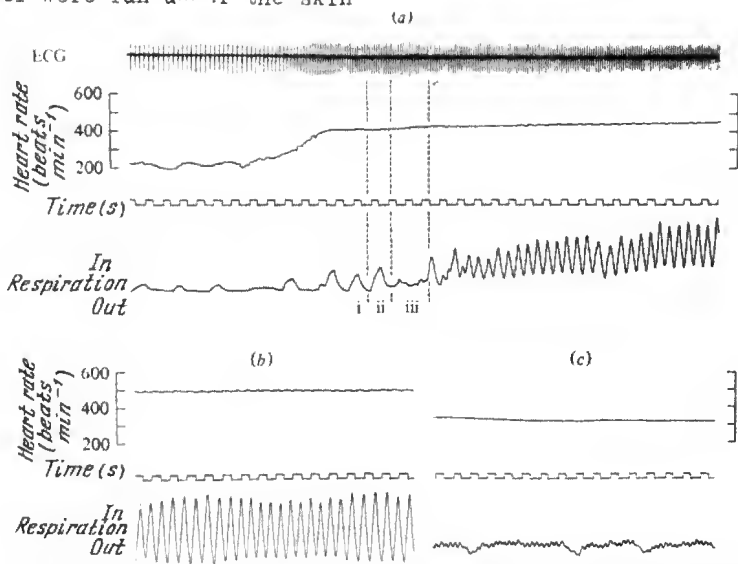


F i g. 6. Traces from a ♀ barnacle goose, mass 1.7 kg, showing heart rate and respiratory frequency obtained from an implanted 2 channel radiotransmitter before, during and after a flight of 11 min 52 s duration (a) Take off; (b) steady flapping flight at 22 ms$^{-1}$, 5 min after take off; (c) 3 min after landing. The vertical dashed lines in (a) indicate when (i) the truck starts to move; (ii) the bird begins to run and flaps its wings; (iii) the bird is airborne (Butler, Woakes, 1980)

because our geese were physically fitter than other birds that had been studied, and/or that they were far less stressed when the data were obtained. None of the measured variables viz heart rate, respiratory frequency, wing beat frequency varied with flight velocity, except when the birds slope
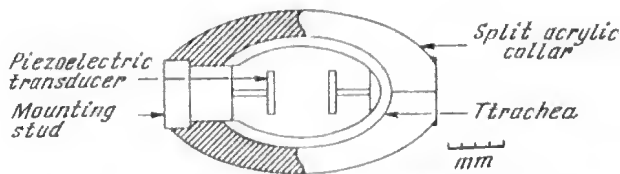
F i g. 7. Diagram of an implantable air flow transducer, shown partially sectioned. The acrylic collar is split into two sections which fit round the trachea. The two sections are held together with 1 mm diameter screws which also retain the mounting studs. These studs project into the lumen of the trachea and carry the piezoelectric transducers (Woakes, Butler, 1979)

soared on the airstream rising over the front of the truck (Fig. 4b). Heart rate was then 50% of the value during flapping flight and respiratory frequency was 70%. This is in accordance with a lower metabolic rate when gliding than during forward flapping flight (Baudinette, Schmidt-Nielsen, 1974). There was a 3:1 correspondence between wing beat frequency and respiratory frequency together with a tight phase locking between the two, which probably persisted throughout the flight (Berger et al., 1970a). The phase relationship was maintained even during transient changes in one of the activities. Perhaps the most important feature of the study is the demonstration that it is possible to obtain physiological data from free flying birds, that are unstressed by the restrictions of a wind tunnel or externally mounted leads or equipment, and yet are close enough to obtain accurate measurements of their air speed and behaviour.

We are now embarking on a programme involving Canada geese, an implantable multichannel transmitter and transducers for measuring tidal volume (Fig. 7) and tracheal oxygen tension (Jansen et al., 1978). This will allow the direct measurement of oxygen uptake and extraction of oxygen in free flying birds during flights of long duration. There will be no externally mounted equipment and the birds will be flying in as near natural conditions as possible. This could be a realistic alternative method to the wind tunnel (Rothe, Nachtigall, 1980) in the study of avian flight. However, a combination of a number of the newer techniques, used with one species of bird, is likely to give the most comprehensive and useful insight into that most pervasive of activities of our feathered friends; flight.

SUMMARY

Metabolism during free flight has been estimated from fat loss and from $CO_2$ production, using the $D_2O^{18}$ method, during flights of several hours duration. However, behaviour of the bird during flight is not always known. Short range radio transmitters have been used to record oxygen uptake and respiratory variables in flying birds, but the flights were only of a few seconds duration.

It has been demonstrated that short range radio transmitters can be used during relatively long flights by keeping the bird close to the receiver. This was achieved by raising bernacle geese from eggs and imprinting them on a human. The "following response" was re-inforced daily so that they would follow the "foster parent". Having established that a particular bird would fly behind a truck with the "foster parent" in the back, a 2 channel radio transmitter was then implanted into it. Thus it was possible to record respiratory frequency and heart rate from birds that were flying at known air velocities for known durations although they were completely unrestrained. With the necessary transducers and transmitters it should be possible to record oxygen uptake and respiratory tidal volume under similar conditions.

R e f e r e n c e s

Bartholomew G.A. - In: Avian Energetics / Ed. by R.A.Paynter. Cambridge, Mass. Nuttal Ornithological Club, 1974,p. 330.
Baudinette R.V., Schmidt-Nielsen K. - Nature, 1974, 248, p. 83-84.
Berger M., Hart J.S. - In: Avian Biology. Vol. IV / Eds. D.S.Farner, J.R.King. N.Y.: Academic Press, 1974, p. 415-477.
Berger M., Roy O.Z., Hart J.S. - Z. vergl. Physiol., 1970a, 66, p. 190-200.
Berger M.,Hart J.S., Roy O.Z. - Z. vergl. Physiol., 1970b, 66, p. 201-214.
Bernstein M.H. - Respir. Physiol., 1976, 26, p. 371-382.
Bernstein M.H., Thomas S.P., Schmidt-Nielsen K. - J. exp. Biol., 1973, 58, p. 401-410.
Brown J.L. The Evolution of Behaviour. N.Y.: W.W.Norton, 1975, p. 628.
Butler P.J. - In: A Handbook on Biotelemetry and Radio Tracking / Eds. C.J.Amlaner, D.W.Macdonald. Oxford: Pergamon Press, 1980, p. 569-577.
Butler P.J. - In: Advances in Physiological Sciences. Vol. 10 / Eds. I.Hutas, L.A.Debreczeni. Oxford: Pergamon Press, 1981, p. 155-164.
Butler P.J. - Exogenous and Endogenous Influences on Metabolic and Neural Control / Eds. A.D.F.Addink, N.Spronk. Oxford: Pergamon Press, 1982,p.105.
Butler P.J., Woakes A.J.- J. exp. Biol.,1980, 85, p. 213-226.
Butler P.J., West N.H.,Jones D.R. - J. exp. Biol., 1977, 71, p. 7-26.
Hails C.J. - Comp. Biochem. Physiol., 1979, 63A, p. 581-585.
Hart J.S., Roy O.Z. -Physiol. Zool.., 1966, 39, p. 291-306.
Hudson D.M., Bernstein M.H. - Fed. Proc., 1978, 37, p. 472.
Hudson D.M., Bernstein M.H. - J. exp. Biol., 1981, 90, p. 267-281.
Jansen T.C., Lafeher N.H., Visser H.K.A. et al. - Med. and Biol. Eng. and Comp., 1978, 16, p. 274-277.
Johnston D.W., McFarlane R.W. - Condor, 1967, 69, p. 156-168.
Kanwisher J.W., Williams T.C., Teal J.M., Lawson K.O. - Auk, 1978, 95, p.288-

LeFebvre E.A. – Auk, 1964, 81, p. 403–416.

Lifson N., McClintock R. – J. Theoret. Biol., 1966, 12, p. 46–74.

Lifson N., Gordon G.B., Visscher M.B., Nier A.O. – J. Biol. Chem., 1949, 180, p. 803–811.

Lorenz K. Studies in Animal and Human Behaviour. Vol. 1. Translated by R. Martin. L., 1970.

Nagy K.A. – Am. J. Physiol., 1980, 238, p. 466–473.

Nisbet I.C.T., Drury W.H., Baird J. – Bird Banding, 1963, 34, p. 107–159.

Ogilvie M.A. Wild geese / Eds. T., A.D.Poyser. Berkhampsted, Herts, 1978.

Pennycuick C.J. – Ibis, 1969, III, p. 525–556.

Rothe H.-J., Nachtigall W. – In: Proc. 17th International Ornithological Congress. Berlin: Deutsche Ornithologen-Gesellschaft, 1980, p. 400–405.

Swan L.W. – Sci. Am., 1961, 205, p. 68–78.

Torre-Bueno J.R. – J. exp. Biol., 1976, 65, p. 471–482.

Torre-Bueno J.R. – In: Respiratory Function in Birds, Adult and Embryonic/Ed. by J.Piiper. Berlin: Springer-Verlag, 1978a, p. 89–94.

Torre-Bueno J.R. – J. exp. Biol., 1978b, 75, p. 231–236.

Torre-Bueno J.R., Larochelle. – J. exp. Biol., 1978, 75, p. 223–229.

Tucker V.A. – Science, 1966, 154, p. 150–151.

Tucker V.A. – J. exp. Biol., 1968, 48, p. 67–87.

Tucker V.A. – Am. J. Physiol., 1972, 222, p. 237–245.

Utter J.M., LeFebvre E.A. – Comp. Biochem. Physiol., 1970, 35, p. 713–719.

Woakes A.J. Biotelemetry and its Application to the Study of Avian Physiology. Ph.D. thesis, University of Birmingham, 1980.

Woakes A.J., Butler P.J. – Biotelemetry, 1975, 2, p. 153–160.

Woakes A.J., Butler P.J. – In: A Handbook on Biotelemetry and Radio Tracking / Eds. C.J.Amlaner, D.W.Macdonald. Oxford: Pergamon Press, 1979, p. 287–292.

ABSTRACTS OF AFTERNOON SYMPOSIA

FORAGING PATTERNS, RESOURCES UTILIZATION AND THE TROPHIC ROLE OF BIRDS

BIRDS, PESTICIDES AND OTHER POLLUTION

ECOLOGICAL MORPHOLOGY

ORIGIN AND EVOLUTION OF BIRD SONG

POPULATIONS OF GAME BIRDS

AVIAN PARASITES

PAIR BONDING

OCEANOGRAPHIC DETERMINATION OF PELAGIC BIRD DISTRIBUTION

LEK BEHAVIOUR

INTRASPECIFIC VARIATIONS

LOSS OF AVIAN HABITAT

THE ORIGIN AND EVOLUTION OF COOPERATIVE BREEDING IN BIRDS

HOLE-NESTING BIRDS

SPECIATION AND EVOLUTION OF SOCIAL BIRDS

STRUCTURE OF FEATHERS

STRUCTURE AND EVOLUTION OF AVIAN CHROMOSOMES

STATUS OF THE WORLD'S CRANE SPECIES

PHYSIOLOGY AND ECOLOGY OF INCUBATION

MOULT

SONG DEVELOPMENT AND SPECIES EVOLUTION

ADAPTATION TO DESERT CONDITIONS

SEABRIDS AND NUTRIENT CYCLES

BIOPHYSICS OF BIRD FLIGHT

GULLS, TERNS AND SKUAS

FORAGING PATTERNS, RESOURCES UTILIZATION AND THE TROPHIC
ROLE OF BIRDS

Convener: R.T.Holmes (USA), co-convener: A.A.Kistchinsky (USSR)


FEEDING PATTERNS OF WOODLAND BIRDS AND THEIR
BIOCENOTIC ROLE

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Composition and quantity of food used by birds are determined by its
quality, accessibility and correlation of birds' food needs and the abundan-
ce of food. When there is no enough food, the whole of its accessible
portion is used. Determining the value of the accessible portion is a
complicated ecological problem. This portion has been shown to in-
crease in direct proportion to the increase in probability of finding food,
its accessibility and its density. It also depends on the spatial distribut-
ion of food, as different substrates (leaves, branches, etc.) are convenient
to different degrees for searching by birds. The methods of evaluation of
convenience of different substrate searching and the results of the corres-
ponding studies are presented. The suggested approach allows the predication
of the removal value of different food groups - seeds, fleshy fruits, insect,
etc.

To evaluate the trophic role of birds in ecosystems, two basic characte-
ristics are used - the quantity of the eaten food and the probability of sur-
vival of potential prey in the absence of birds feeding on them. The second
characteristic is rarely used in biocenotic studies, therefore it seems im-
possible to obtain the true idea of the role of birds and other animals in
ecosystems. Of a particularly great importance is the correct evaluation of
the effect caused by the seed dispersion by birds. While studying the after-
effect of predation, an important ability of birds to switch over to mass
prey species is considered. This shortens the delay period and leads to the
effective control of prey abundance. On the whole, birds contribute to
higher resistance of both undisturbed forest ecosystems and those changed
by the man. The role of birds is most appreciable on plant succession.


IMPACT OF INSECTIVOROUS BIRDS ON THE POPULATION PROCESSES
OF THEIR PREY, WITH SPECIAL REFERENCE TO THE CODLING MOTH

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In most studies of the effects of insectivorous birds on their prey num-
bers, lack of information on other mortalities means that the effects of
birds on the population dynamics of their prey are unknown. Studies on the
population dynamics of codling moth (Cydia pomonella) show that predation by
birds is of great importance when larvae are exposed to predation for seve-
ral months.

Codling moth larvae are exposed to predation by birds when they mature
and build cocoons beneath the bark of apple trees. This predation has little

effect on larvae that develop without delay to give a second or third generation in warm summers. However, larvae overwintering in diapause are exposed to bird predation for about eight months; woodpeckers (<u>Dryobates spp</u>) in Canada, silvereyes (<u>Zosterops lateralis</u>) in New Zealand, and tits (<u>Parus spp</u>) in Europe take 50-95% of such larvae. The intensity of predation in any one year is spatially density dependent, but from year to year it depends on fluctuations in the numbers of birds, as well as larval density.

THE IMPACT OF BIRD PREDATION ON THE PATTERNS OF LEAF
CONSUMPTION BY FOREST INSECTS

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Even though birds exhibit both numerical and functional responses to increasing prey densities, they seem to be generally ineffective in controlling outbreaks of herbivorous insects (especially <u>Lepidoptera larvae</u>). Recent evidence, however, suggests that birds do exert significant predation pressure on endemic populations of their prey. Although this pressure may help to further suppress insect populations and to extend the periods between outbreaks, we propose that the more important influence of such heavy predation on low density prey is to exert natural selection for prey adaptations, many of which result in restrictions or modifications on the patterns of insect feeding. Adaptations such as crypsis, aposematism, restricted choice of feeding substrates, rigid feeding schedules, tissue (food) preferences, and even the organization of some life cycle features may be favored by natural selection due to predation; these in turn determine or affect the patterns and amounts of leaf consumption by these herbivorous insects. In this paper, we review the evidence for this hypothesis, using data primarily from our studies of bird/insect interactions in a northern hardwoods forest in New Hampshire, USA. From this analysis of the adaptive syndromes of herbivorous insects and of bird foraging behavior and pressure, we suggest further observations and experiments that will test the hypothesis that bird predation has been a major organizing force on the trophic-dynamics of herbivorous forest insects.

S Y M P O S I U M
<u>BIRDS, PESTICIDES AND OTHER POLLUTION</u>
Convener: R.W.Risebrough, USA

USE OF MANAGEMENT TECHNIQUES TO PROMOTE THE RECOVERY
OF AN ENDANGERED POPULATION OF <u>FALCO PEREGRINUS</u>

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Peregrine Falcons have experienced severe declines in population size throughout most of their cosmopolitan range since the late 1940's. In central

coastal California the decline has mainly been due to DDE-induced eggshell thinning, resulting in lower productivity and in recruitment failures. By 1970, only one known territory was occupied (by a lone male) along the 400-mile coastline which includes 25 historical nesting territories. By 1981,as a result of reduced environmental levels of DDE and of management of the existing population since 1977, six coastal eyries were occupied. The management techniques, first developed by the Pergrine Fund for endangered peregrine populations but suitable for other raptors, enables maintenance of existing territories and expansion of the remnant population into areas of former range and historical nesting territories. This management includes: 1) captive incubation of thinshelled wild eggs; 2) fostering of the young from captive-incubated wild eggs; 3) introduction of young from captive breeding falcons into wild nests; 4) hacking of young at currently unoccupied historical nesting torritories; and 5) supplemental feeding of wild falcons by providing a clean food source (domestic pigeons). However, unless DDE levels in peregrines and in the environment are permanently reduced, this population, like all peregrine populations, continues to face extinction, or reliance upon management on a permanent basis.

IMPACT ON THE AVIFAUNA OF PESTICIDE USE IN THE STATE
OF RIO GRANDE DO SUL, BRAZIL

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The use of insecticides, including chlorinated hydrocarbons that are no longer applied in many northern hemisphere countries, is generally believed to be increasing in South America. The effects on the avifauna are as yet largely undocumented. In the state of Rio Grande do Sul, Brazil, there is widespread pesticide use, but there is also increasing public concern over the effects of the indiscriminate use of many of these pesticides. Data are presented in this paper on the levels of the organochlorine pesticides in representative species of the avifauna. Nothura maculosa, a common inhabitant of the principal land use types in the state (soya cultivation, rice cultivation, pastureland, and uninhabited grasslands), was used as an indicator of the relative levels of contamination in these areas. Data on organochlorine levels in raptors and aquatic birds with close relatives in the northern hemisphere permit an assessment both of general contamination levels, and the effects of these compounds on local species.

# POLLUTANT EFFECTS ON OSPREY

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Many factors were considered as contributing causes to the initial decline of Osprey population in the north-eastern United States: encroachment by man, loss of habitat, reduction of the food supply, as well as a varity of pollutant chemicals. The work of Dr.Spitzer and his colleagues has conclusively demonstrated that only one pollutant, was responsible, DDE, the environmentally    stable derivative of the insecticide DDT.The DDE effects were associated with shell thinning; Dr.Spitzer's studies have further demonstrated that productivity was significantly lowered when the degree of shell thinning was not sufficient to cause breakage. Thus there is not necessarily a "threshold-of-effect" level of DDE upon productivity, indicating that factors other than egg breakage are involved...

Other case histories were reviewed, including the Bald Eagle, <u>Haliaeetus leucocephalus,</u> in northwestern Ontario, the White-tailed Eagle, <u>H.albicilla,</u> in Scandinavia, Finland, and the German Democratic Republic, the Brown Pelican, <u>Pelecanus occidentalis,</u> in southern California, and the Peregrine Falcon, <u>Falco peregrinus</u>, in Great Britain and arctic North America. In each case reproductive failures, usually with regional population declined, had been  associated with eggshell thinning; in the majority, an inverse relationship had been demonstrated between shell thickness and DDE levels. In each case either a partial or a complete recovery occurred with a decline of environmental levels of DDE. The influence of other environmental factors, including pollutants such as PCBs, other synthetic organics, and trace elements, had either been minimal and not demonstrable, or had been discounted.

The conclusions of these field studies have been supported by an extensive series of laboratory investigations which have shown that DDE causes shell thinning in many bird species, particularly raptorial and fish-eating species, but including doves and ducks, at levels frequently found in the environment. Other organochlorines, including the common pesticides and the PCBs, were found not to cause the effect.

We can therefore conclude with reasonable certainty that the shell thinning which has been documented in many populations, and the associated population declines of some of these, have been caused only by DDE.

Following the ending of DDT use, environmental levels of DDE are falling in northern countries. In one area, the central coastal region of California, levels have remained too high in recent years to permit the sucessful reproduction of Peregrine Falcons. Comparison of the relative amounts of DDE, $p,p'$-DDT, mirex, dieldrin and heptachlor epoxide in unhatched eggs of this population with those in comparable samples from Greenland and from arctic and interior Alaska, have lead to the conclusion that the majority of the DDE currently accumulated by this population originated from DDE originally applied in California rather than from DDT recently used in Latin America.

ECOLOGICAL MORPHOLOGY

Convener: B.Leisler (FRG), co-convener: F.Ya.Dzerzhinsky (USSR)

Comparative studies in eco-morphology try to understand the relationship between morphological variation in animals and their ecology. As almost all features of an organism are interdependent and are results of compromises such studies require a good knowledge of the life history of the species investigated and information about phylogenetic relationships among the species. One objective of the symposium was to concentrate on some historical-evolutionary aspects in eco-morphological studies.

DRINKING BEHAVIOR AND FEEDING ADAPTATIONS IN PARROTS
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Within Parrots, at least four different drinking methods can be distinguished, each of them characteristic for an entire subfamily, irrespective of the feeding specializations of the particular species. Each subfamily is also characterized by a specific basic morphology of the tongue, bill, and mouth cavity. The various basic morphological types of the feeding apparatus have been evolved as feeding adaptations from that in an ancestor adapted to seed-eating. During this first stage of adaptive radiation, not only were the feeding apparatus and feeding method fundamentally transformed, but with it also the drinking method. The following stages of adaptive radiation, taking place within the subfamilies, did not affect the drinking methods. The various drinking methods evolved as a by-product of the adaptive changes connected with feeding specializations and were not under the control of selection forces associated with drinking. Although there are no clear eco-morphological correlations to be found for the drinking methods, the distribution of certain species may be affected by their drinking method. The drinking behavior in Parrots illustrates the need in eco-morphological studies to distinguish between those structures and behaviors that evolved under the control of a selective force not related to the environment to which they are presently adapted.

THE FORAGING OF INSECTIVOROUS AND FRUGIVOROUS BIRDS
AND THE IMPORTANCE OF MORPHOLOGY TO BEHAVIOR
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The diminution of competition among animals is frequently attributed to the differences in foraging behaviors of the potentially competing species. Field studies are frequently done which demonstrate that, for example,birds feed on different foods, at different heights, or on different parts of the vegetation. However, the trophic apparatus, and those parts of the bird that assist the trophic apparatus in obtaining or minipulating food, is limited in its ability. Thus the behaviors we observe may not be a resuit or competition.

There exist possible conflicts between behaviors induced by ecological constraints and those allowed by morphology. The foraging behaviors observed in the field are most often attributed to environmental causes—competition, weather, and food supply, for instance. Morphological aspects are typically considered in only the broadest sense (hummingbirds east nectar and insects but cannot eat berries), yet they may be at least as important as the ecological factors which are measured in more detail.

This study looks at an example of an insectivorous species and a frugivorous species and weighs their ecological and morphological constraints.

## SOME ASPECTS OF THE ADAPTATION OF THE FEEDING APPARATUS IN ROLLERS (CORACII)

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Some new aspects of feeding adaptations in rollers were discovered with the help of morphofunctional analysis of their feeding apparatus. The original adaptations that developed in this group (Coraciidae, Brachypteraciidae and Leptosomatidae) were for catching relatively large insects in flight. This key adaptation included automatic mechanisms insuring an effective grip on the prey and protecting the eyes against contact with the prey. The superficial orbital oponeurosis has a basic role in the eye protection mechanism; it is tensed automatically by the protracted upper jaw as the bill opens.The eyes are covered by the raised lower eyelid which contains cartilage. Vibrissa-like feathers form an elastic screen providing passive protection. The strengthened palate is crucial for catching flying insects. It assimilates the impact energy of the prey and uses it for an automatic sharp closing of the mandible. The ossified postorbital ligament is essential for this action. Strongly developed maxillopalatines and prefrontals seem to damp surplus energy. The main features of this key adaptation are retained in all species of rollers. They are most specialized in Eurystumus, Leptosomus discolor of Madagascar catches relatively large sluggish animals on branches. The jaw apparatus of Uratelornis shows adaptations to pecking (e.g., to obtain termites). Coracias has the most generalized jaw apparatus.

## S Y M P O S I U M
## ORIGIN AND EVOLUTION OF BIRD SONG
Convener: L.Baptista (USA), co-convener: G.N.Simkin, USSR

## BIRD SONG AND AVIAN SYSTEMATICS

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Bird song is useful in avian systematics primarily at the level of the species. Birds use song in mate selection and in species recognition. Song provides an experimental method of determining species limits in some birds. Experimental tests of mate choice in females finches(Vidua) and grebes

(Aechmophorus) have shown that females are attracted to conspicific sexual song and not to the song of closely related species. A less critical test of species distinctiveness is playback to males which sometimes respond to other species (especially if they are interspecifically territorial) and sometimes do not respond as strongly to songs of various population dialects as to their own local population. Song is learned in most passerines, so by itself it is no indicator of genetic distinctiveness at the species level. Moreover, song differences among populations do not necessarily indicate genetic or systematic differences, for many freely dispersing birds have song dialects (learned). It is necessary to associate song differences with morphological or other genetically-determined differences among populations to determine species limits.

In systematics above the species level, song is useful as one among many characters, and has not the significance that we find at the species level. Members of a species group, genus or subfamily often have similar song, but even here exceptions occur with some species having songs unlike their closest genetic relatives. At higher levels song is even less reliable as an indicator of evolutionary relationship; flamingos and geese both honk, but biochemical and paleontological studies point to other groups (storks or waders) as the possible sister group of the flamingos. Song appears to be increasingly less useful in reconstructing cladistic or evolutionary relationships at the higher levels of systematics. The complex of morphological features under more direct genetic control reflect lineages with Hennigian or other logical phyletic techniques that deduce evolutionary history. In contrast, song (at least in passeriformes) is learned in block, either from one parent or from several neighboring conspecifics. The processes of cultural tradition differ from those of genetic or biological evolution in several ways (lack of successive meiotic genome sampling of the preceding generation(s), lack of additive genetic differentiation over time) that render questionable any higher-order biosystematics based primarily on song.

CENTRAL NERVOUS PROCESSING OF BIRD SONG
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The contribution of neurophysiology to our understanding of evolution of bird song may be its explanation of the central nervous mechanisms of song analysis. The principles discovered can elucidate the functioning of intraspecific communication and of species recognition.

The only information that nerve cells within the ear of a bird receive about a song are the frequency and intensity components that it contains. All the other information about conspecifity and individual recognition, has to be worked out by central nervous mechanisms. These mechanisms occur at different levels of the auditory pathway as the acoustic signal proceeds through it. The higher the station in the auditory pathway, the more detailed is the information about an acoustic signal within single neurons. Although it is not likely that one will find single cells responsible for the recognition of single song phrases, we can find neurons whose responses represent important

parts of these phrases like the dynamics of frequency modulation in trills, and bandwidth of frequency in aggressive calls and song parts.

Another important neurophysiological aspects is the neural plasticity during song learning. It can be shown that learning different types of song influences the response behavior of central neurons and thus determines central mechanisms of song recognition.

## VOCAL LEARNING STRATEGIES IN BIRDS

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Birds are highly vocal creatures and males (sometimes females) of many species learn to sing just as humans learn to speak. This phenomenon has received wide-spread attention and study, yet the functions of vocal learning and the selective forces favoring this learning continue to be debated. These functions and forces may not be unitary, however, for the consequences of vocal learning vary remarkably among different bird species. Insights into the vocal learning strategies of birds will be discussed by examining:

1) different vocal development and population consequences in closely related songbird species (Troglodytidae);

2) the marked difference in micro-geographical variation with functionally different song types within a species (Parulidae);

3) differences in song development among the imitative oscines (e.g., Troglodytidae, Emberizidae) and the non-imitative (?) non-oscines (e.g., Tyrannidae);

4) disparity in both size of song repertoire and volume of neural song control areas between two populations of the same songbird species (Marsh Wren, Cistothorus palustris).

## SYSTEMATICS AND CARDUELINAE SONGS

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Detailed studies of the systems of acoustical communication in Carduelinae (13 species from the genera Acanthis, Spinus, Carduelis, Chloris, Pyrrhula, Serinus) let assess the applicability of different categories of acoustical signals for systematic purposes and make apparent some trends in their evolution. Our results suggest, that one should use polythetic approach to the bioacoustic criteria to make them into suitable tools for investigations in systematics on different levels of taxonomic scale. Songs, because of their complex structure and high degree of variability, are of little use for systematic studies above the species level. The study of calls which are phylogenetically more ancient, of simple structure, less liable to geographical and individual variations permit to reveal both species-specific and group characters with more ease. In order to determinate whether the forms under discussion may be considered specifically distinct, it is convenient to study "call-songs", males' courtship calls, females' calls preceding copulation. For definition of the taxa at the generic and familial levels it

is expedient to apply the signals of such functional categories which are of little or no connection with reproduction and retain ancestral, common for the group features: nonspecialized aggressive and alarm calls, mobbing calls, flight calls, signals for flock integration. Strict distinction between main categories of vocalization, i.e. calls and songs, does not exist. On the ground of our data and in consideration of the principles developed by G.N.Simkin (1982) we come to conclusion that song is the product of phylogenesis of the complex multifunctional demonstration which forms as a rule on the basis of species-specific call system as a result of ritualization. The most simple form of Carduelinae songs is "call-song", genetically preformed unsophisticated vocalization with sexual motivation, characteristic only for males. The main song type is "advertising song" which serves first of all as a means of attraction and stimulation of females. During phylogenesis it develops on the basis of several categories of the calls: flock calls, call notes, males' calls accompanying courtship and territorial demonstrations. Calls, which turned into song elements, retain their structure unaltered or have certain modifications of physical patterns. Song becomes complicated also by developing specific song elements. Complex structure of Carduelinae "advertising song" serves principally to secure individual marking of the male and to characterize his physiological state and social status.

S Y M P O S I U M
POPULATIONS OF GAME BIRDS
Convener: S.G.Priklonsky (USSR), co-convener: P.Rajala (Finland)

COMMON EIDER NEAR COASTS OF EAST EUROPE
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Thanks to a system of protection measures, fulfilled in the USSR, and to careful attitude towards this species in the northern countries of West Europe there is an abundance of common eider in Estonia, on the White, Barents and Pechora Seas in 1970-ies there was 50-70 thou. adult birds, of which 10-17 thou. inhabited Estonia, the rest-Arctic ocean seas. Their abundance seems to be close to the optimum level in the north, the increase in number on the Baltic Sea continued. They began nesting off the north-west coast of the Black Sea. It is suggested, that 3 geographic populations - one of the White Sea and two of the Barents Sea - inhabit the north.

Geographical features of seasonal distribution, morphometric differences and variants of male dress and other features of common eider define them as belonging to a certain population. Despite a small annual mortality and comparatively small number of eggs in a clutch, yearly variance in a number of common eider nesting on different archipelagoes often reach 50-60% and sometimes more. This is due to changes in bird distribution on aquatic area, which is inhabited by a population in a year cycle. The weather conditions and sometimes other ecological reasons are usually the reasons for these changes. Mostly young birds seem to perform migrations since females, which nested earlier, show significant nest site fidelity.

The abundance of common eider is negatively influenced by predation of big sea gulls and hooded crows, in some regions by helminthosis and by other factors.

EUROPEAN WOODCOCK POPULATIONS, ABUNDANCE
MIGRATION AND UTILIZATION
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The main breeding areas of the European Woodcock (<u>Scolopax rusticola</u>) extent through Northern and especially Eastern Europe and Asia, the main wintering areas lay in Western Europe, roughly bordered by the January isotherm of 1.5°C. Due to a considerable variation in the direction of migration the winter quarters of the breeding populations are not sharp to define.

Breeding records and especially hunting statistics point to shifting abundances in different parts of the woodcocks range during this and the last century, for which climatic changes might have played an important role.

The woodcock is a valuable game bird throughout its range. The hunting pressure is highest in the wintering areas of western Europe. According to band recoveries an overall average of a fifth of the European population may be taken by hunters annually. The main harvest is done during fall and winter, some countries traditionally harvest courting males in spring and summer, as in other polygamous game birds.

Recent research projects, coordinated by the "International Waterfowl Research Bureau", deal mainly with habitat preferences, breeding biology, banding calculations and kill-statistics. The latter two providing aspects of the size of the European populations.

THE POPULATION ASPECTS OF THE COOT'S ECOLOGY IN WEST SIBERIA
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The numerous Coot's population is distributed in the steppe and wood-steppe zones of West Siberia. The main body of Siberian Coots stay for wintering on the Caspian Sea and on the inner lakes of the Middle Asia. In spring the first Coots reach West Siberia in the second half of April. Prenesting period is very short. The first egg is laid not more than 2-5 days after arriving. Mass laying of eggs takes place in the first decade of May. Mass hatching was observed on the average in the last decade of May and at the beginning of the first decade of June. The young Coots begin to fly at the end of July. The yearly production of the local Coots population is high. The average clutch size during the 1970-1980 years was $8.8 \pm 0.11$ eggs hatch size - $6.8 \pm 0.09$ nestlings, the surviving of nestlings - 77.3%. During June - August the population is represented by adult nesting birds by young and one year old birds (who do not reproduce this year) in correlation 1:2:4. Broods, local and migrate one year old birds and moulting birds (adult and one year old) are isolated in space. The migration takes place during the

end of August - the middle of October. The migration of birds of different ages is isolated and takes place at different dates. During the autumn hunting season hunters shot about 90-95% birds of one year old. It is connected with their approachability and long stay in the nest area. Altogether 0.4-0.5 million Coots were shot in West Siberia during the hunting season. This constitutes an average of 10% of the total amount of the Coots population (3.3 -4.3 millions birds).

GENERAL FEATURES OF FINNISH TETRAONID POPULATIONS
DURING RECENT DECADES
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Since 1964 large-scale route censuses of tetraonids have been carried out annually in Finland in order to monitor the population densities as well as the structures of populations. The route census results have indicated a marked decline in tetraonid populations. Capercaillie populations especially have clearly decreased; the Black Grouse and Hazel Grouse populations also show significant decline. These negative trends have been most marked in central Finland, which still has the best populations. Northern Finland has not suffered any significant decrease.

By combining the results of route censuses with game questionnaires it is possible to backdate the tetraonid population estimates to 1946. During the 35-year period the Capercaillie populations have decreased by about 45%. The highest populations were recorded in 1953 and 1962.

The Finnish Capercaillie populations can be divided into three asynchronously fluctuating regions, which fit well with the presumed areas of different subspecies. The Black Grouse populations reveal the existence of four fluctuation regions, while the Hazel Grouse and the Willow Grouse populations show no such regions.

Percentages of juveniles, brood sizes, adult sex ratios and proportions of hens with broods are compared at different phases of the fluctuation.


S Y M P O S I U M
AVIAN PARASITES
Convener: V.Baruš, (ČSSR), co-convener: K.Ryzhikov, (USSR)

THEORETICAL AND PRACTICAL ASPECTS OF RESEARCH
ON BIRD PARASITES
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The accumulation of data on the parasites (in the widest sense) of various taxa and whole systematic groups of avian hosts in various geographic regions has lead to their confrontation and synthesis in subsequent stages of development of ornithology and parasitology. The synthesis on the level of the

host-parasite relationships has made it possible to formulate, enlarge, supplement, or precise certain regularities of general importance (such as a larger number of parasitophyletic rules or laws; the specificity or hostality phenomenon; reservoir or parathenic parasitism; zoogeographic classification, and others). The study and evaluation of the parasite-host-environment relationships in which the hosts are avian taxa (populations) yields new data which enrich not only ornithology but which often clarify complex epidemiological and epizootological problems, the maintenance and circulation of such pathoergonts as viruses, bacteria, mycotic organisms, protozoans, helminths and arthropods. The many-sided applicability of such knowledge is documented by the solution of problems concerning diseases of man and domestic animals which show marked natural focality (both transmissive). Quite a new angle to view the dynamic evaluation of the relationships between birds and their parasites is provided by the complex study of the process of their synanthropization and synurbanization. Due to the variability of external factors and the differential adaptability of both components these processes, taking place quite recently, are considerably diversified. It is a matter of learning the general laws that govern a short period of evolution of the interaction between the human population and those of birds and their parasites, involving valuable practical aspects.

## REGULARITIES OF ANSERIFORM HELMINTH FAUNA

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Among the helminth fauna of Anseriform birds are trematodes belonging to the family Echinostomatidae which will be used to establish generalities in the development of helminth species composition in the Anseriformes.

Ecological factors are most important with hydrotopical species being predominant in the helminth fauna of these birds. Similar helminths in different hosts result from similar ecologies, especially feeding. Phylogenetic relationships is also of some importance in the helminth parasites of Anseriform species.

Helminths having an ecology different from that being typical for this family usually acquire new hosts although this is not characteristic for this group. Changes in host ecology enlarge the species composition of its helminth parasites. Host specialization results in the evolution of new higher taxonomic groups of helminths. Abrupt changes in the morphology and biology of echinostomatids occurred in non-intestinal (liver, kidney, bursa Fabricii, etc.) species which is not typical for the family.

Different modes of feeding, e.g., in mallards, increases the number of parasites. Among the Anseriform helminths, are found certain groups in the process of active speciation. Members of these groups are found in hosts belonging to different avian orders and vertebrate classes which favors the process of speciation.

PARASITIC ARTHROPODS IN BIRDS

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The role of birds as hosts of various arthropods (except extrasomatic ni-
dicoles) is discussed.

Temporary parasites, alternately staying on hosts and in free nature, are
represented by exophilic Diptera and exo- and endophilic Acarina. Periodical
parasites showing permanent parasitism of certain developmental stage, both
mites and flies, are less frequent.

Permanent parasites with constant parasitism of all developmental stages
constitute the biggest group. Within the parasitocenosis of a host, the pa-
rasitic arthropods from a pterocenosis which, together with protozoans and
helminths, is an important part of the bird somatocenosis. According to the
localization of the parasites, an exo- and endosomatocenosis may be distin-
guished. The main components of the pterocenosis are the plumicolous and
syringicolous Acarina and plumicolous Mallophaga. The exosomatocenosis comp-
rises various mites and biting lice which live on the skin surface. The louse-
flies form a transient category. The representatives of cutaneous, subcuta-
neous, nasocavital, pulmonar and tissue parasitic mites are components of an
endosomatocenosis.

The possibilities are discussed of using arthropods parasitic on birds to
determine the phylogenetic relationships of their hosts. The knowledge of the
parasitic arthropods as vectors of arboviruses is of great practical import-
ance.


PARASITOPHYLETIC ASPECTS OF ANATID BIRD LIFE

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The paper includes an analysis of species composition of Mallophaga in
Anatinae. Studied the host specificity. A fairly strict predestination of
certain species and groups of Mallophaga towards their host was shown. On
the basis of this regularity, the phylogenetic relationships between groups
of Anatinae, as well as their relations to other birds, were analysed.


ROLE OF SEASONAL BIRDS' MIGRATIONS
IN THE HELMINTH FAUNA FORMATION

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A migration effect on the formation of helminthofaunistic complex in birds
has been studied for nematodes of Calidris species with the application of
matrix analysis.

The nematode fauna of Calidris has been shown to be dependent on the site
of location of these birds and the season of year and to a lesser extent on
the species. This enabled us to use for the analysis the general lists of
nematodes parasitic in all Calidris species in 11 regions of the USSR.

Intersections measure matrix has been made, inclusions measure matrix has been constructed on its basis. For the analysis of the latter directed graph with "67% of banality"has been applied. It has been shown that the nematode fauna of Calidris birds of Baltic region and Turkmenia is more "exotic" and "original" than that of Calidris birds of the mouth of Yenisei river, region of Lake Baikal and Yakutia is most "banal".

On the basis of the intersections measure matrix a similarity measure matrix analyzed by means of graph "similarity 53%" has been made. It can be assumed judging from the composition of the nematode fauna that Calidris birds nesting at the Ob inlet migrats along the Caspian-Iranian route; those nesting at the mouth of Lena River along Khinganian route and ths birds nesting at the mouth of Yenisei River - along both routes. The nematode fauna of Calidris nesting on Chucotka is similar to that of this group nesting in Primorye Territory and on the island of the Bering Sea. This is indicative of a fact that Calidris birds migrate for wintering along these two routes.

Therefore the helminth fauna composition of Calidris birds is dependent on their routes of migration. The analysis of Calidris nematode fauna also demonstrates that the helminthofaunistic data may supplement and sometimes develop our knowledge about the routes of bird migrations.


WILD WATERFOWL AS HELMINTH RESERVOIRS TO DOMESTIC FOWL
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The paper includes the results of investigations on the helminth fauna in domestic ducks and geese and in wild waterfowl that was investigated in the same water reservoir where also domestic fowl was reared. The total number of helminth species in domestic and wild birds was the same (59 species)when the majority of species (40 species) was found in both groups of birds.

Examined the dynamics of infestation by helminths in domestic ducks. The infestation starts during the first 24 hours after the young bird is released on the water reservoir. Cestodes (Hymenolepididae) are the first ascertained parasites. The infestation is realized by eating up crustaceans, the intermediate hosts of these helminths. Crustaceans are infected by eating up cestode eggs, excreted by wild waterfowl living on the reservoir. It was found that a young duck eats up a fairly high number of crustaceans and of other invertebrates being intermediate hosts of helminths. With respect to that, the infestation cannot be avoided even at a low percentage of infestation of temporary hosts by helminth larvae. Molluscs have a greater epizootological role in helminth exchange between wild and domestic waterfowl. They are intermediate hosts of all trematodes parasitizing these birds, and they are reservoir hosts of hymenolepidid cestodes. 11-19% examined Mollusca were infested by cysticercoids of Hymenolepididae.

ON THE APPLICATION OF HELMINTHOLOGICAL DATA IN
ELUCIDATING THE PECULIARITIES OF BIRD DISTRIBUTION

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While studying the characteristics of the helminth fauna of different
ecological groups of Charadriiformes birds we have made an attempt to as-
sociate them with the pattern of distribution of these birds.

The material has been collected in the territory of central regions of
the European part of the USSR. Of 23 Charadriiformes species from the forest
zone 18 species (182 specimens) belonging to 3 ecological groups (waterside,
meadow and forest) have been studied. In waterside birds 9 parasite species
were found, mean number of species per bird is 1.5; mean number of helminths-
26.3 individuals; 93% of all studied birds were infected. The figures for
meadow birds are respectively 42.0; 1.2; 40.0; 90%; those for forest species
are 14.0; 0.9; 19.0 and 100%. 6 helminth species are found only in waterside,
34 only in meadow and 6 only in forest species. 3 helminth species are found
in all ecological groups, 7 in waterside and meadow, 7 in meadow and forest,
and 3 in waterside and forest groups.

The individual parasite groups having marine invertebrates as the inter-
mediate hosts disappeared from birds of the forest zone and were replaced
by the species freshwater and terrestrial invertebrates as intermediate
hosts. The helminth fauna of modern ecological groups of Charadriiformes
birds was ultimately formed in several definite foci under the control of
biocenotic factors. Differences in the parasite faunas of different ecolo-
gical groups of Charadriiform birds allow the assumption that the distribut-
ion of these birds occur by the colonization of waterside biotopes of fresh-
water reservoirs, meadow and lastly forests from marine coasts.


S Y M P O S I U M
PAIR BONDING
Convener: G.Orians (USA), co-convener: W.Wickler (FRG)


CHOICE OF BONDING PARTNER

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Since the choice of the individual with which to mate can have a large ef-
fect on the reproductive success of the chooser, we can expect selection to
have produced strategies for optimizing mate choice. In birds, as in most
animals, females usually have primary responsibility for mate choice. Females
should be influenced in mate choice by any male characteristic that (a) has
an important effect on female fitness, (b) is variable from male to male, and
(c) is accurately assessable prior to mating. Females might base their choice
on the genetic quality of males, in order to secure good genes for their off-
spring. However, because fitness has low heritability and is difficult to
assess, choice on genetic quality is unlikely to be favored if alternative
strategies are available. Choice on parental care quality is likely to be

adaptive in those species in which males furnish parental care, provided that there is some basis for assessing future male parental care quality prior to mating. Choice on the quality of resources provided by males is clearly adaptive whenever males provide resources; in birds, such resources may include nests, nuptial gifts of food, and access to feeding and nesting territories. Mixed strategies, in which more than one male characteristic influences choice, are highly probable.

In the Red-winged Blackbird (Agelaius phoeniceus) males defend territories in which harems of females nest and gather part of the food resources for breeding. Data from several studies indicates that territory quality is much more important for female choice than is the quality of the male. Harem sizes in successive years on arbitrary territories are strongly correlated, whether or not the same male is holding the space. In addition, there is no correlation between harem sizes and such measures of male guarding ability as the attack rates of males on potential predators nor any correlation between the attack strength of the male and the rate of predation on nests within his territory. Harem sizes increase with the age of the male as well. In some Redwing populations age is also correlated with the amount of feeding of nestlings by the male but in others it is not, so that the reasons for the preference shown by females for older males are not yet clear. Nor is it clear how much genetic variance in male quality is present in this and other species of birds.

CHOOSING AND KEEPING A PARTNER
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**Great Tits** males defend territories that contain both nest sites and all of the food resources used by the pair and its offspring during the breeding season. Extensive data from a population of individually marked birds show that older birds breed sooner in the spring, have larger clutch sizes, and higher fledging success and post-fledging survival than do younger birds. Therefore it is advantageous for all birds to mate with older individuals. Pairs are not formed randomly with respect to age of partner. Rather, most older birds are mated to other older birds and young birds are mated to young birds. The experience of the mate is much more important to females than it is to males; pairs consisting of an old male and a young female are as successful as pairs consisting of two old birds, whereas pairs consisting of a young male and an old female do nearly as poorly as pairs consisting of two young birds.

Great Tits do not move far between breeding seasons so that if both members of a breeding pair are alive the following year they are likely to be aware of one another's presence. Nonetheless between 30 and 40% of pairs in which both partners survived divorce between years. The breeding success of pairs which breed together in successive years is compared with the success of birds which change partners. Birds which fail to raise a brood (the main reason for which is usually predation) are more likely to change than birds which are successful. Part of the reason for this is that birds which lose

a brood tend to nest further away from the nest site of the previous year than do birds which are successful. The breeding success of birds in relation to moving and changing partner is compared and selective value of such behaviour is discussed.

PAIR BONDS AND DIVORCE AMONG CORVIDS
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Most West-European Corvid species (Corvus corone, Corvus frugilegus, Corvus monedula, Pica pica) maintain a continued monogamous pair-bond, i.e. they do not switch mates between successive breeding seasons. When divorces do occur they usually include a switch of territory as well as of mate. The readiness to accept a new mate seems to be facilitated by sex-specific tolerance. Males are likely to tolerate female intruders in their territory and territorial females also do not always expel intruding males. In this way extra-marital courtship is sometimes induced.

Pair members which seldom attack intruders of the opposite sex also often fail to assist their mate in chasing. The proportion of individuals showing sex-specific aggression and weak or absent co-operation in attack vary within and between species. Even within an individual's lifetime the tendency to favour a certain mate by chasing potential rivals can change.

If prior knowledge of the territory is particularly important for the success of a newly settled bird, then individuals would benefit by deserting their mates to pair with a widowed territorial resident. However, if an established pair does better in unfamiliar terrain than a newly formed pair, even if one partner knows the area, then divorce should be rare. Among the family Corvidae some species move into new breeding sites as pairs and seldom divorce their spouses, while in others individuals readily divorce their mates to form bonds with widowed birds on better territories. Connecting the character of the pair-bond to reproductive output and co-operation in reproductive activities are important first steps to a functional explanation of intra- and interspecific differences in co-operation and persistence of mate choice.

CONFLICT IN REPRODUCTIVE EFFORT WITHIN AND
BETWEEN PAIR BONDS
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Time expended in courtship feeding, nest building, incubating, advertizing for more mates, seeking outside copulations, feeding young and defending territory compete for the limited time available to a mated bird. Because of their lower energy commitment to gametes males find themselves in situations where reduced expenditures within an existing bond may lead to enhanced reproductive success more often than do females. In this family of about 95 species there is no reported case of courtship feeding, feeding of the incubating female by the male, or of incubation by males. In only two species are males known to participate in nest building. In contrast, males of every

monogamous species so far studied help feed nestlings and fledglings. Among polygynous species, males feed nestlings and fledglings in some species, but do not do so in other species. Males that do feed, usually favor nestlings in their primary nests, but can be induced to feed at secondary nests if the young are growing more poorly there or if there are more young in the secondary nest than in the primary nest. Thus, male investment in nestling care is highly variable and apparently well-adjusted to immediate conditions. This is in striking contrast to the patterns that are invariate, or nearly so, in the entire family.

These patterns could be explained in one of several ways. First, it is possible that it is not advantageous to either males or females for males to incubate, feed the incubating female or build nests in any of the species. Second, it could be advantageous to males not to perform those activities but females would benefit if they did. Females could be in a "cruel bind" because they are unable, at the time of pair formation, to assess the probability that their mates will perform such parental behavior. By the time it is evident that they will not, it is too late to desert. Moreover, they would face the same assessment problem with any new mate. Third, it could be advantageous to both males and females for males to incubate and feed incubating females but the requisite components of the behavior have not yet arisen in those species.

It is, as present, impossible to distinguish between these possibilities because the lack of variability in male behavior prevents us from making the most useful comparisons. However, assembling additional comparative information may reveal new patterns that are more informative and may suggest experiments not currently evident.


S Y M P O S I U M
OCEANOGRAPHIC DETERMINATION OF PELAGIC BIRD DISTRIBUTION
Convener: G.Hunt (USA), co-convener: R.G.B.Brown (Canada)

SEABIRD DISTRIBUTION AT SEA IN RELATION TO WEATHER
AND WATER MASS CHARACTERISTICS
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The distribution of birds at sea in the Southern Ocean south of Africa correlates poorly with each of the following environmental parameters: barometric pressure; salinity; air temperature; water temperature; wind strength; and wave height. However, principal component analysis applied to the environmental parameters defines two potentially useful factors (weather and water mass), but the birds' distribution still does not appear to be correlated strongly with abiotic environmental features. A variety of possible combinations of cause-effect interactions among the physical parameters (barometric pressure, temperature and wind) revealed no highly significant linear relationships between seabird distribution and weather. Linear models ex-

plain a very small proportion of the spatial variation in seabird community
structure. Thus, the use of abiotic environmental features as predictors of
seabird distribution seems limited, which suggests that pelagic seabirds are
distributed randomly at sea or their distribution is non-random as a conse-
quence of a combination of biogeographical history, food requirements, breed-
ing period and locale, and physical environmental features. This hypothesis
may only be testable with a complex stochastic model, and we lack sufficient
data for a number of important variables necessary for the construction of
such a model. At present, the only meaningful patterns discernible in the
distribution of Southern Ocean seabirds relate to spatio-temporal separation
by diet and feeding method.

THE DISTRIBUTION OF SEA-BIRDS DURING AN YEAR AND THE CAUSES
OF ITS CONCENTRATION OF THE GEORGE'S BANK

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Analysis of the results of investigations undertaken by the authors permit
the following conclusions:

1. Large nesting and feeding concentrations of sea-birds are formed in re-
gions or in separate local sea areas having high biological productivity.
Birds contribute to this productivity directly by fertilization with their
excrements which speed up development of the feeding base.

2. Analysis of changes of the biomass in phyto-zooplankton, ichthyofauna
and cephalopods revealed its annual development and reproduction on the Ge-
orge's Bank and its attraction for a large number of sea-birds in this region.

3. The 140.000 recorded individual sea-birds on the George's Bank belon-
ged to 40 species, of which 36 nest in the northern and 4 in the southern
Hemisphere. Thus, the sea-birds of the area belong to two quite different
avifaunas - northerns and southerns.

4. The species-composition of migrating sea-birds changes year by year.
The quantitative ratio of individuals of each species changes also and leads
to a considerable modification of the avifauna most years.

5. The composition of the sea-birds on the George s Bank depends not only
on trophic factors, but also on periods of wandering and migration which
are governed by endogenous rhythms of each species.

6. In ecological investigation of marine avifaunas, special attention
should be given to the change of quantitative rations between "northerns"
and "southerns" because the phenomenon of replacement of one fauna by the
other typical to the region of the George's Bank must be found in other
oceanic areas. This suggestion is supported by the presence of transequato-
rial migrants in both the southern and northern hemispheres.

SEABIRDS DISTRIBUTION IN THE NORTH SEA AND ADJACENT
NORTH ATLANTIC OCEAN: OCEANOGRAPHIC AND ECOLOGICAL INTERPRETATION
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Seabirds were counted for one-hour-periods, from both moving and stationary oceanographic ships: R.V.Meteor and R.V.Anton Dohrn,FRG, and R.V.Mechelen, Belgium.

The distribution of pelagic seabirds is clearly related to the different water masses, determined by their oceanographic characteristics: salinity and temperature. A group of species which are almost absent in the North Sea water and are bound to Atlantic water: Gannet (<u>Sula bassana</u>) 1.4 individual per station; Great Skua (<u>Stercorarius skua</u>), 4 ind.; alcids (<u>Fratercula arctia</u>, <u>Uria aalge</u> and <u>Alca torda</u>) 20 to 60 ind. per station. Two species are present in both Atlantic and North Sea water: Fulmar (<u>Fulmarus glacialis</u>), respectively 40 to 70 and less than 20 ind. per station; Kittiwake (<u>Rissa tridactyla</u>), resp. 15 to 60 and less than 10.

The main difference between Atlantic and North Sea waters is attributed to their ecological structure. A complete food web is developed in Atlantic water, with high densities of zooplankton, fishes and pelagic seabirds, and low density of bacteria. In North Sea water, however, for comparable levels of primary production, a high density of bacteria reflects that the organic matter is mainly recycled by bacteria, and the higher levels of the food web, zooplankton, fishes and pelagic seabirds, are present at low densities.

It is concluded that, in zones presenting a good oceanographic homogeneity, pelagic seabirds can be used as bioindicator for the ecological structure of marine ecosystems, combined with a simple measurement of phytoplankton density, such as chlorophyll.

THE SIGNIFICANCE OF OCEANOGRAPHIC DOMAINS AND FRONTS FOR
SEABIRD DISTRIBUTION IN THE BERING SEA
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The shelf waters of the southeastern Bering Sea are separated by fronts into three distinct oceanographic domains; the inner or coastal domain, the middle domain, and the outer domain at approximately the 50, 100 and 200 m isobaths. The inner domain is characterized by a uniformly mixed water column, the middle domain by a two-layer water column separated by a sharp thermocline, and the outer domain by a multilayer system.

The density and community structure of seabirds differs between domains. Northern Fulmars (<u>Fulmaris glacialis</u>), Fork-tailed Storm-Petrels (<u>Oceanodroma furcata</u>), Black-legged Kittiwakes (<u>Rissa tridactyla</u>) and Red-legged Kittiwakes (<u>R.brevirostris</u>) are most common at the shelf-edge and outer domain,

while murres (Uria sp.) and auklets are more plentiful over the middle domain. Shearwaters (Puffinus sp., mostly P.tenuirostris) are most abundant in the inner domain. In general, the outer domain is dominated by surface foragers taking pelagic fish and invertebrates, the middle domain is dominated by alcids, and in the inner domain, birds dependent on epibenthic fish and euphausiids predominate. While there are major differences in bird populations between domains, there are also differences in bird densities between fronts and interfrontal areas, due to occasional high concentrations of birds over fronts. Species composition of such aggregations vary, although murres and shear-waters are frequently conspicuous.

S Y M P O S I U M
LEK BEHAVIOUR
Convener: J.Kruijt (The Netherlands), oo-convener: A.Lill (Australia)

POSSIBLE SELECTION PRESSURES INVOLVED IN THE EVOLUTION
OF LEK BEHAVIOUR
A.Lill
Psychology and Zoology Departments Monash University, Clayton
Victoria, Australia .

Most attempts to identify the likely selection pressures which influenced the initial stages of the evolution of display clustering in promiscuous male birds have been speculative, a posteriori adjuncts to investigations, often of high quality, but with different objectives. The recent modest trend towards the derivation and field testing of predictions about such selection pressures stemming from various theories of lek evolution should be continued and expanded.

Any comprehensive theory of the evolution of display clustering must explain the continuum of male spatial dispersions ranging from uniform fields to leks observed in promiscuous birds. A useful starting point is to consider the possible costs and benefits of male display clustering to both sexes, the underlying premises involved and the main predictions which follow if these costs and benefits are real. This application of current sociobiological ideas and knowledge to the problem of the evolution of spacing in promiscuous male birds should elucidate the kinds of data needed to understand that process.

To illustrate the approach, we can consider just one of the many examples of possible costs and benefits of male clustering to both sexes which were examined. This was the idea that clustering involves a greater time and energy investment in inter-male aggression. The main premises underlying this supposed cost of clustering to males are (I) that clustering increases the frequency and/or duration and/or intensity of inter-male aggressive interactions and (II) that the resultant greater time/energy expenditure on aggression reduces male fitness. Therefore if this is a real cost for males, the time/energy investment on aggression per male should increase with cluster size within species and should result in relatively lower courtship and/or self-maintenance investment levels. If unbalanced by sexual benefits of clustering, this should be reflected in decreasing mean male lifetime reproductive success with increasing cluster size.

1026

These predicted trends in aggression and courtship levels occur in Golden-headed manakins but do not always lead to reduced male mating success (Lill, 1976). In bowerbirds, bower construction and maintenance are expensive activities and bower destruction and decoration theft by neighbours is common. The uniform dispersion of males may be adaptive in reducing these behaviours (Donaghey, 1981; Pruett-Jones and Pruett-Jones, 1982). The toothbilled bowerbird which does not build a vulnerable bower is the only, or one of the few bowerbird species in which male display clustering probably occurs (D.Frith, pers. comm.).

Although display clustering may often involve benefits for both sexes, it may sometimes evolve as a default phenomenon i.e. there are not necessarily any socially determined advantages for either sex, although there may be socially mediated costs. Thus males may be forced to cluster because females cluster to exploit heterogenous resources or males may cluster in a few, restricted, predator-proof sites.

Many of the predictions about possible costs and benefits of male display clustering which were developed are testable, but the relevant data remain to be gathered. The most fruitful testing ground for these predictions lies in intra-specific comparisons in promiscuous species with locally variable male dispersion patterns.

SEXUAL SELECTION IN BIRD LEKS
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The intensity of sexual selection in birds that display on leks is higher than in monogamous species and than in most polygynous species where the male provides resources or a nesting site. A theoretical population genetics model of Wade and Arnold (1980) indicates the potential for sexual selection in a population as the variance in breeding success/ mean success . The model was used to test whether the potential for sexual selection differed in species with different mating systems. Especially in lekking species, a few males account for most of the success, and most males have no success. The results showed the greatest relative variance in success, and thus the greatest potential genetic sexual selection, in males of the lekking species, and the lowest in the monogamous species.

The implied variation among bird species in the intensity of sexual selection generally parallels the observed evolutionary results of sexual selection in sexual dimorphism in body size, male ornamentation, or both. Sexual dimorphism is greater on average in the lekking species in several families of birds, though not in all.

Behavioral mechanisms that underlie evolutionary sexual selection include male-male competition and the choice of a mate by the female. In several lekking birds, female mate choice appears to be directly or indirectly for the more aggressive males. Intrasexual competition may explain most evolved instances of sexual selection in lekking birds. Alternative sexual strategies such as noncourtship rape and sociosexual parasitism by deceiving apparently noncompetitive males generally are uncommon in birds.

# ECOLOGICAL DETERMINANTS OF ALTERNATIVE MATING STRATEGIES
## IN RUFFS (PHILOMACHUS PUGNAX)

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Sex ratio of Ruffs in the Dutch breeding areas seems to be subject to considerable changes every season. In early spring, when females copulate, sex ratio is biased towards females; in late spring, when females nest, it is biased towards males. I concluded that females copulate on migration, which would be adaptive since conditions for male competition seem to be best in the south of the breeding area, whereas food conditions for chicks seem to be most favourable in the extreme north. This hypothesis implies a temporal and spatial segregation between copulation and egg fertilization (Van Rhijn, 1983). In the present paper the evolution of this presumed segregation is discussed. On the basis of the diversity of mating systems within the family Scolopacidae (Pitelka et al., 1974), and a number of other features like sexual size dimorphism and sperm morphology (McFarlane, 1963), females of ancestral species were supposed to lay two clutches of eggs, the first being incubated by their former mates, and the second by themselves. At present similar mating systems are known in Calidris alba (Parmelee, 1970) and C. temminckii (Hildén, 1975). In this presumed ancestral mating system females may be expected to exert two different kinds of choices for mates. For their first clutches they were supposed to prefer males with good parental qualities, for their second clutches males with good genes. Thus, females may select disruptively in the male population, which could be a cause in the evolution of role differentiation in male Ruffs (Hogan-Warburg, 1966; Van Rhijn, 1973).

# SEXUAL SELECTION AND MATE CHOICE IN
## BLACK GROUSE (TETRAO TETRIX L.)

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On leks or arenas, Black Grouse males can neither monopolize females, nor do they provide resources for them. Yet, mating is clearly non-random and thus appears to be due to female choice. The main aspect of female preference is that they mate much more often with males whose territories are clustered on the center of the arena than with males defending marginal territories. Ultimate and proximate factors, underlying female choice, are discussed.

With regard to ultimate factors, we argue that males whose territories are small, and clustered on the center of the arena, are in a better position than marginal males, to exploit the heterogeneously distributed resources of very large home ranges, because they tend to synchronize activities and leave their territories outside periods of display. Furthermore, males in a cluster are usually several years old, and have to be in good physical

condition in order to face the severe competition between males for terri-
tories on the center of the arena. These properties may reflect high quality
of central males and, if heritable, females should be expected to choose a
mating partner from the center rather than one of the marginal males. We
showed experimentally that females were actually more attracted to a group
of 6 stuffed males, than one of 3, which suggests that a cluster as such is
attractive to females.

However, other differences between clustered males must also be involved,
because copulations are often very unequally divided over the males of a
cluster. Copulation success is positively correlated with the time during
which males have defended a territory on the arena. This suggests that suc-
cessful males possess behavioural and/or morphological characteristics which
are attractive to females.

In this paper we draw attention to one possible behavioural factor: va-
riability of rookooing, the vocalization of males which is produced almost
continuously during display, especially when females are present on the
arena. Rookooing consists of strings of phrases which may be produced for
minutes on end. Each phrase of 2.5 to 3 sec. can be subdivided in an inflat-
ion section during which the oesophagal pouch is filled with air, and a
convulsive section during which the pouch is partially deflated and rein-
flated in rapid succession. Convulsive sections are highly stereotyped(about
1.25 sec.), but the duration of inflation sections varies among males from
about 1.1 to 1.4 sec. As a result, males with short inflation sections pro-
duce a higher rate of rookooing phrases, which is further accentuated because
such males seldom interrupt rookooing when females are nearby. In two seas-
ons, the male with the highest copulation success was also the male which
produced short inflation sections and high rates of rookooing phrases. Thus,
although proof is lacking, females possibly discriminate between males on
the basis of such differences in rookooing. Functionally, this discriminat-
ion would become understandable if differences between males in rate of
phrase production reflect heritable quality differences between males.


S Y M P O S I U M
INTRASPECIFIC VARIATIONS
Convener: F.C.James (USA), co-convener: V.M.Loskot (USSR)


THE GEOGRAPHY OF ALLELIC FREQUENCIES IN THE WESTERN
FLYCATCHER (EMPIDONAX DIFFICILIS)

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Starch gel electrophoresis was used to survey genetic loci in approxima-
tely 200 Western Flycatchers from 10 populations in the western United Sta-
tes. Traditional biosystematic treatment had demonstrated significant geogra-
phic variation in the Empidonax difficilis complex that approaches the species

level. Of 39 scorable loci surveyed, 12 were polymorphic. Seven other systems could not be scored. The data permit the calculation of genetic distances and the construction of dendrograms which depict relationships among populations. The allelic frequency data for certain loci correlate closely with patterns of geographic variation in size, color, and structure of song syllables. Similar data for other loci appear to be geographically random. The new genic information will be integrated with a previously proposed hypothesis on the mode of sibling speciation in Empidonax flycatchers.

TRANSPLANT EXPERIMENTS AND MORPHOLOGICAL VARIATION
IN BLACKBIRDS (ICTERIDAE)
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Many species of birds breeding in the eastern and central United States have the same pattern of intraspecific size variation. Body size is smallest in the warm humid southeast. Larger birds occur northward and westward where the climate is cooler and/or drier. In the Red-winged Blackbird (Agelaius phoeniceus) there is also allometric bill shape variation. The extremes are the small slender-billed population in southeastern Florida and the large conical-billed population in central Colorado. We transplanted eggs during incubation between nests in northern and southern Florida and the phenotypic development of these nestlings was modified toward that of the foster population. In a second experiment eggs were transplanted from Colorado to Minnesota. The extent of the nongenetic component of intraspecific morphological variation in birds will be discussed.

TEMPORAL AND GEOGRAPHIC CHANGES IN THE BREEDING RANGE OF
THE BLUE MORPH OF ANSER CAERULESCENS
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Canada

Cooch (1962) traced the expansion of the blue morph of Anser caerulescens from 1929 to 1961 and made predictions as to the continued expansion of this morph. In the 20 years since then the numbers of A.c. caerulescens have doubled. Most of the increase has occurred in Hudson Bay, Canada, south of 64°N. latitude. Although the blue morph is spreading westward as predicted, the rate of increase in the proportion of blue morphs in colonies where it was previously established has slowed or reversed. A hypothesis has been developed to explain these changes.

# MORPHISM AND HYBRIDIZATION OF WHEATEARS OENANTHE HISPANICA AND OE. PLESCHANKA

Vladimir Loskot

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Field studies conducted in 1965-1979 and the study of collections (over 900 specimens) resulted in new data on intraspecific variability of Oenanthe hispanica and Oe. pleschanka. A combination of discrete colour characters of plumage allowed discrimination of local populations and groups of populations with distinct proportions of morphs. A hybridization zone of these wheatears was the subject of a special study. Contrary to Northern Iran where parapatric hybridization was described (Haffer, 1977), situation in Transcaucasia and Mangyshlak Peninsula is an example of sympatric hybridization (or zone overlap and hybridization). No data were found supporting either the role of the Mangyshlak population in maintaining the proportion of whitethroated morph over the remaining area of Oe.pleschanka or a gradual reduction of the frequency of this morph outside Mangyshlak Peninsula (Panov, Ivanitzky, 1975). No evidence was obtained of any significant westward gene flow from a narrow hybridization zone into the area of Oe. hispanica. Hence the leading role of hybridization in the origin of morphism in these species of wheatears (Haffer, 1977) is not supported. A hypothesis of ancestral Oe. hispanica being primarily polymorphic in plumage coloration and origin of Oe. pleschanka from a most pigmentated eastern form of this ancestral species seems more plausible.

# GEOGRAPHICAL VARIATION IN SOME AMASON FOREST BIRDS

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Geographical variation in several widespread and common species of Amazon forest birds is studied through computer analyses of various mensural and color characters. The resulting contour maps for individual characters and for character complexes illustrate regional gradients in geographical character variation within Amazonia. In some cases these patterns permit meaningful application of the taxonomic subspecies concept. Broad rivers are barriers to dispersal for species inhabiting the forest interior. These barriers to gene flow introduce steps or breaks in the regional gradients of geographically variable characters. The extent of these breaks varies considerably between species. The breaks disappear in the headwater regions of the Amazon tributaties, where rivers are smaller and channel meandering permits easy gene flow across them. The results are interpreted in light of different ecological habits of species studied, differing ecological conditions across Amazonia, and the changes in vegetation cover during the last two million years.

LOSS OF AVIAN HABITAT

Convener: R.A.McCabe (USA), co-convener: I.Ahlen (Sweden)


LOSS OF OPEN PEATLAND AND SOME OTHER OPEN HABITATS
IN SWEDEN AND THE EFFECT ON THE BIRD FAUNA

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Draining of wetlands has taken place in Sweden since the 19th century. Until 1970 about 1 million, out of a total area of 7 million, hectares of peatland have been drained for different purposes. During the last decade the demands for wetland drainage has increased rapidly. It has been proposed that more than 75% of the peatlands in South and Central Sweden and in the coastal parts of North Sweden should be drained for forestry or fuel peat production. The effects on the bird fauna of these activities have often shown to be drastic. Peatlands which are wet and treeless lose most of the waterfowls and wader-species within a year after draining. Twenty years later all the original species have been found to be replaced by other species on fertile peatlands. On less productive sites the process is slower. The density of wetland birds varies markedly between different areas according to many different habitat factors. The major part of all wetland birds is found on a limited proportion of the peatland area. This emphasizes the urgent need of a conservation programme.

Other open habitats such as heathland, shrubland and wetland pastures are also lost as important avian habitats due to afforestation, cultivation and free successional growth, with effects on various groups of birds as a consequence.


EFFECTS OF HABITAT FRAGMENTATION ON SOUTH
FINNISH FOREST BIRDS

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Formerly continuous forest habitats have been increasingly fragmented owing to human economic activities during the past decades. In this paper quantitative data, mainly based on extensive censuses of land birds on the Aland Islands (60°N, 20°E) in 1926-27 and in 1975-80, are used to specify and quantify effects of fragmentation on forest bird populations.

Two major topics will be addressed:

1. Edge effect increases the numbers of a large and heterogeneous group of forest passerines that are favoured by bushes and saplings in the forest. Increasing fragmentation has a negative effect on species demanding large and continuous forest tracts. Several nonpasserines belong to this group.

2. Studies of insular habitats indicate minimum area requirements of different species. Prevalence functions based on census data are an effective method for this purpose; these functions express relative densities in areas

of different size and show whether the area of a habitat fragment has an effect on densities or not.

The significance of forest fragmentation as a cause of population decrease will be discussed. The importance of quantitative data for identifying ecological factors leading to declines of bird populations is stressed.

HABITAT CHANGES IN BRITISH SCRUBLANDS AND THEIR
INFLUENCE OF BREEDING BIRD COMMUNITIES
Robert J. Fuller
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Hertfordshire, UK

In Britain, scrub is a localised type of vegetation yet many species of birds depend on it as a breeding habitat. Not only is the habitat an ephemeral one, as a seral stage in various successions, but also it is frequently controlled or totally destroyed in order to improve grazing lands and to reclaim land for a wide range of developments.

The aim of this paper will be as follows:

1. To illustrate for several types of scrub the rate of change of bird species composition and specificity of species to stages of the scrub succession.

2. To outline the impact of scrub removal on bird communities from various quantitative case studies.

3. To predict the ornithological impact of selective srub removal.

The paper will be based on a wide set of quantitative data drawn from the files of the British Trust for Ornithology's Common Birds Census and from a detailed study of the dynamics of scrub bird communities on the chalk escarpment of the Chiltern Hills, England.

THE DECLINE OF MEADOW-BIRDS IN THE AGRICULTURAL
LAND IN HOLLAND
Albert J. Beintema
Research Institute for Nature Management, the Netherlands

In the Netherlands, densely populated for centuries, practically all habitats are man-made. Thus, agricultural activities in the typical polderlands have created ideal conditions for 'meadow-birds'. In the low, moist grasslands some wader species breed in numbers not known elsewhere. As a typical example, about 80% of all Europe's Blacktailed Godwits breed in this small country.

This situation is now gradually destroyed again, by means of lowering of water tables, and intensifying of dairy farming in all its facets. It can be shown in a mathematical model that a reduction of hatching success alone is sufficient to explain the present decline. The model, which has been tested for 5 species, works with daily survival rates of nests, basically determined by predation, but heavily modified by cattle densities, grazing periods, and timing and frequency of mechanical management, such as mowing. The model allows for relaying after nestloss within certain limits, depending on the population dynamics of the species. Thus, it can be shown that species differ in their vulnerability towards agricultural pressure. Vulnerability increases

in the order: Oystercatcher, Lapwing, Godwit, Redshank, Ruff. The first is
still increasing, benefited by increased biological production, the last
has already practically disappeared from this country, apart from nature
reserves.

When in a certain area the management is known in detail, the model can
predict which species will be able to maintain their populations. Finally,
the model predicts that when the ultimate agricultural intensity, as propa-
gated by official bodies, will be reached nationwide, there will be no
meadow-bird habitat left in the Netherlands, outside reserves.

THE LOSS OF A LARGE COLONY OF YELLOW HEADED BLACKBIRDS
(XANTHOCEPHALUS XANTHOCEPHALUS) FROM SOUTHERN WISCONSIN
Robert A. McCabe
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The yellow headed blackbird is a marsh nesting species that builds its
nests in vegetation primarily cattail (Typha latifolia). Such marshes were
scattered throughout this state but agriculture, urbanization, landfills
and other forms of development have caused such wetlands to disappear. Bet-
ween 1947 and 1951 a yellow headed blackbird colony was studied on a wetland
15 miles north of Madison, Wisconsin. During that period (5 years) 243 nests
were located; those nests produced 444 fledglings with a nest success overall
of 71%. Only about 2/3 of the entire wetland was in the study block. The es-
timated population in this block in 1948 was 400 birds including a small
nonbreeding cohort.

This area of wetland including a shallow lake had gone dry several times
in recorded history. On this basis the owner was able to take legal action
to drain the entire area. In spite of detailed testimony on its value as a
wetland the court upheld the owner and he drained the marsh. In 3 years
after drainage 99% of the marsh land birds disappeared including the yellow
headed blackbird colony. Also lost were populations of coot (Fulica ameri-
cana), Florida gallinule (Gallinula chloropus), black tern (Chlidonias niger),
ruddy duck (Oxyura jamaicensis), red-winged blackbird (Agelaius phoeiceus)
and long billed marsh wren (Cistothorus palustris) and numberous other birds
and mammals including a thriving population of muskrats (Ondrata zibethicus).

RAPTOR POPULATIONS DECIMATED BY FARMING IN
SEMI ARID KALAHARI
Richard Liversidge
McGregor Museum, Kimberley, South Africa

Strip counts along dry "riverine" habitat in the southern Kalahari in-
dicates that the raptor population is drastically reduced where no protect-
ion is afforded.

Farming activities prompted by traditional anti-raptor sentiment with
consequent shooting of raptors and deterioration of the habitat due to ex-
tensive stock farming have resulted in:

a) reduction of the commonest vulture to more than one tenth normal
numbers;

b) reduction of eagle populatios from one tenth to nearly 1/200 normal levels;

c) reduction of the commonest hawk to one third of normal numbers;

d) no reduction in the smallest shrike-sized hawk.


HABITAT LOSS AND ITS ROLE IN THE DECLINE OF THE
PUERTO RICAN PARROT (AMAZONA VITTATA)
James W. Wiley
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Since 1968 we have been measuring habitat needs of the endangered Puerto Rican parrot. In this research we have traced the history of habitat loss in Puerto Rico through the substantial records maintained by individuals and the island agencies (primarily Commonwealth and Spanish agriculture departments and the U.S. Forest Service) and by interviewing "old-timers" familiar with the parrot and its former status. Major causes of habitat loss have been identified as have their relationship to the parrot's decline.

In the Luquillo Forest habitat utilization by the remnant parrot population has been extensively investigated. The forest has been sampled for availability of nesting sites: 1216 trees in 27.3 ha of the Luquillo Forest were climbed to determine presence and suitability of cavities for parrot nests. This revealed that there were very few adequate sites available. Further investigations have revealed several management (e.g. timber stand improvement) policies and selective cutting of potential and actual nest trees (e.g. for parrot chicks or honey) that substantially reduced available nesting habitat.


S Y M P O S I U M
THE ORIGIN AND EVOLUTION OF COOPERATIVE
BREEDING IN BIRDS
Convener: R.P.Balda, USA

Cooperative breeding refers to situations where adult birds regularly take part in helping to rear offsprings which are not their own. Helping behavior occurs in over 200 species of birds, which inhabit ecological conditions varying from forests through savannahs to desert. Helping thus poses questions for ecologists concerned with the role of the environment in shaping major features of avian social organizations. Cooperative behavior also appears to contradict the theory of natural selection, since helpers behave in a way that incurs a cost to themselves while providing a benefit to the recipients (the breeders). Cooperatively breeding species thus provide excellent examples for testing various sociobiological hypotheses for the evolution of "altruism".

In this symposium, five very different examples of helping behavior will be examined in detail. The comparative approach will serve to clarify the similarities, and the differences, in the selective forces that have determined cooperative breeding strategies.

## GROWTH OF TERRITORIES IN THE FLORIDA SCRUB JAY

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The Florida Scrub Jay (Aphelocoma c. coerulescens) is a cooperative breeder in which many pairs receive assistance from non-breeding helpers, and pairs with helpers raise more young. Preliminary analysis showed that territory size and family size are positively correlated (Woolfenden and Fitzpatrick,1978). A positive correlation does not demonstrate a causal relationship, howerver, because large territories could harbor individuals or resources capable of producing more young than do smaller territories. A critical test for our territorial hypothesis is to measure territory size within families that have varied in size over several years. We now have 25 families that meet these criteria, and 22 of the 25 (88%) showed territorial growth between family sizes of 2 and 3, and 17 of 23 (74%) between family sizes of 3 and 4. The possibility exists that territories simply have increased in size from one year to the next because of stability of the pair, and that additions to the family are coincidental. Testing it we compared changes in territory size between consecutive seasons within families whose size and breeding pair remained unchanged. Of 43 such cases, 19 showed slight increase, 17 slight decrease, and 7 no appreciable change in territory size.

Territorial budding, in which a helper becomes a breeder in a segment of its natal territory, is an opportunity restricted to males. Because it seems that male helpers can gain more from territorial growth than female helpers, we examined territorial growth and sex of helpers. For pairs with only one, older helper territory size was significantly larger if the helper was a male (mean = 11.5, n = 14) than if a female (mean = 7.9, n = 11). These data strengthen the hypothesis that Florida Scrub Jay helpers gain directly from helping breeders raise more young.

## COOPERATIVE BREEDING IN THE MEXICAN JAY

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Social organization in the Mexican Jay (Aphelocoma ultramarina) was studied in 1958 and 1969-82. Social units of 5-25 jays defend group territories in pine-oak woodland from Arizona and Texas south through central Mexico. One to four pairs breed separately within each territory (plural breeding). Nestlings are fed communally by parents and non-breeding helpers, which may constitute 50% of a unit. Fledglings are fed communally by all parents "reciprocally". Within units jays compete for food in winter, and their relationships can be expressed as a linear dominance hierarchy with few reversals. When breeding, pairs in a unit rob each other's nest lining and eggs. Mutual benefit from sharing tasks augmented by indirect fitness due to close relatedness, helps to maintain the social system.

PINON JAY FLOCKS AND PATCHY PINON PINES

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Pinon Jays (Gymnorhinus cyanocephalus) live year-round in large (70-150 birds) tightly knit flocks. Flocks are composed mainly of extended family units. The timing of most events in the yearly cycle is set by the size of the Pinon Pine cone crop of the previous fall. The high energy pine seeds serve as the major food in the winter and spring. Seeds are retrieved from subterranean caches made on a communal area. Pairs breed in colonies where mutual nest defense and helping behavior occurs. During October and November some yearlings switch flocks. Those that remain in their home flock have several options open to them during the breeding season. (1) Most yearlings form pair bonds and court but do not nest. (2) Some yearling females nest with older males. (3) Some yearling males help raise their siblings. (4) Some pairs nest with varying degrees of success (5) Some yearling males nest with older females. The relative merits of each of these options will be discussed with an emphasis on those young males that help.

THE ADAPTIVE SIGNIFICANCE OF COOPERATIVE BREEDING IN THE
PIED KINGFISHER (CERYLE RUDIS)

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Pied Kingfishers in breeding colonies can adopt a number of different strategies. They can be helpers or breeders (1); as helpers they can raise siblings or strangers (2); and as breeders they can accept or reject helpers (3).

1. The decision whether to breed or to help depends mainly on the availability of females since the sex ratio ie 1.8 males: 1 female.

2. The helpers prefer. to feed close kin ("primary helpers") but if none are around they try to feed the young of non-relatives ("secondary helpers"). Primary helpers tend to invest more, and consequently have a lower survival rate, than secondary helpers, who frequently breed in the same place they helped the year before, sometimes with the female they helped.

3. If the breeders' time and energy are sufficient to rear most of their young alone, they tend to reject potential secondary helpers. If not, they will accept them. This can be shown by comparing birds living under different ecological conditions and by manipulating clutch sizes and food supply. Primary helpers are tolerated under all conditions.

The adaptive significance of the helpers' and breeders' behavior will be discussed by comparing the inclusive fitness of birds following these different strategies.

COOPERATIVE COURTSHIP: ANOTHER TYPE OF HELPING BEHAVIOR

Mercedes S. Foster

Mussum Sea++᠕ᴖ. U.S. Fish and Wildlife Service National
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Cooperative courtship behavior has been reported for at least six species of birds, though preliminary evidence indicates that it probably occurs in several others, as well. Such behavior generally involves the performance of advertising vocalizations and precopulatory displays, and the defense of the copulating pair from rivals. In all instances so far reported, the helpers are males of lek-breeding species. For several, reasons, social systems in which the pair bond is short and courting males are closely spaced are preadapted for this type of behavior. Its evolution, however, will depend upon associated increases in fitnesses of the individuals involved. Possible benefits accruing to the donor of the help are an increase in inclusive fitness through kin selection, increase in his own probability of mating, increased probability of inheriting the mating site, and improvement of subsequent reproductive performance through learning. Benefits to a recipient of the help may include attraction of greater numbers of females, increased copulatory success, and in soms instances, a decrsase in disruption of copulation.


SYMPOSIUM

## HOLE-NESTING BIRDS

Convener: C.M.Perrins (UK), co-convsner: H.Löhrl (FRG)

DIMENSIONS OF NEST-HOLES OCCUPIED BY GREAT TITS AND
EVALUATION OF THEIR FUNCTIONAL SIGNIFICANCE

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The Great Tit Parus major nests in a very wide variety of holes. Nevertheless, significant preferences (particular hole depth, wide internal diameter) ars shown to exist. The prsferences were examined by putting up pairs of boxes of different dimensions, close together and examining the frequencies with which each type of box was occupied. Presented with boxes with internal diametsrs of 11.5, 14.0 and 20.0 cm, most Great tits preferred ths largest box. They also preferred deep (14 cm: 19 cm) boxes to shallow ones and built deeper nests in ths deep boxes. It is thought that the birds get improved insulation from the deeper nest which saves them energy during incubation. However, they also need to keep their nest at a considerable distance from the nest entrance if they are to be beyond the reach of predators, especially those such as the Marten (Martes martes) which may reach in and pull out young if the nest is too close to the entrance. Hsnce a bird cannot risk building the best size of nest (for incubation purposes) if the nest cavity is too small.

The Great Tit shows little preference for the size of nest sntrance (provided ths hole is reasonably small); offered choices of holes of 30, 32

and 38 mm. diameter, the Great Tit showed no significant preference for any one of them. This was not the case for the smaller species all of which when offered the choice between holes of 32 and 26 mm. diameter, showed strong preference for the latter. This again may be related to predation since very few predators can get through a hole of 26 mm. diameter; even the Weasel Mustela nivalis is usually excluded. The Weasel can however, easily get through a hole of 30 mm. diameter. This is the smallest hole through which a Great Tit can easily get. Hence there is little advantage to the Great Tit in choosing nest-sites with small holes since the Weasel, which can be a serious predator, can get through any hole that the Tit can. The smaller species may, in addition, get some advantage from the use of sites with small entrances in that the Great Tit is excluded; at times it may be a considerable nuisance to them if it can enter their nest. Hence presumably the smaller species can reduce the risk of competition with the Great Tit by choosing the smaller holes when they are available.

Some hole-nesting species such as the Pied Flycatcher, Ficedula hypoleuca, defend a very small area around the nest-site rather than a "normal" territory. The Great Tit however, defends a normal territory, often of about 0.5-1.0 ha. With a very high production of young, there seem to be, at least in some years in some areas, a number of birds which are unable to obtain such a territory.

REPRODUCTIVE SUCCESS OF THE GREAT TIT PARUS MAJOR
IN RELATION TO ITS TERRITORIAL STATUS
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The Great Tit is a territorial species, although in some years pairs are observed that breed without having defended a territory around the breeding hole. Some of these 'intruders' defend a territory adjacent to the study plot where no nestboxes are available, and are called territorial intruders. Others have not been observed to defend a territory anywhere, and typically build their nest very rapidly. These are called real intruders. I will argue that these birds are floaters that attempt to breed after the territorial birds have started. 1980 was a year with numerous intruders. In a study plot of 11 ha in a wood near Antwerpen 46 first clutches were found; 27 belonged to birds territorial on the study plot, 7 to territorial intruders, and the other 12 to real intruders.

All intruders were yearlings. Territorial intruders laid later than territorial birds, but were equally succesfull. Real intruders were less succesfull than both other groups, and I will discuss what factors influenced their reproductive success.

Owing to the large number of intruders it was possible to analyse the effect intruders have on the reproductive success of the host pair. Territorial birds with intruders lay a smaller clutch, have a lower nesting success and hence fledge fewer young compared to birds without intruders. Some reasons herefore will be suggested.

Finally I will discuss why Great Tits should defend a territory, taking into account data from years without intruders.

# REPRODUCTIVE STRATEGIES OF TITS IN MEDITERRANEAN CONTINENTAL AND INSULAR HABITATS

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On the mainland there are five species of Parus Blue Tit, Great Tit, Coal Tit, Marsh Tit, P.palustris, and Crested Tit, P.cristatus. The last two of these nest at the lowest densities and are absent from Corsica.

Corsica has 14.7 pairs of Blue Tits per 10 ha. as opposed to 4.7 on the mainland. It may be that one of the explanations for the higher densities on the island is that there is a lowered inter - specific competition (a number of insectivorous species are absent), but that, as a result intra-specific competition may be more intense.

The average date of 1st egg on Corsica is 2-3 weeks later than on the mainland (13 May and 25 April) and the clutch size is also much lower (6.0 eggs and 8.8 eggs). Breeding success is also poorer, on average 20 pairs in the mainland raise 130 young compared with 56 raised by the same number of pairs on Corsica. Such variation is compensated for by the fact that adult birds live longer on Corsica; 60% of the breeding birds are older than one year old compared with only 36% on the mainland. Differences of the same order of magnitude were also found for the Great Tit and the Coal Tit.

S Y M P O S I U M

SPECIATION AND EVOLUTION OF SOCIAL BIRDS

Convener: L.L.Short (USA), co-convener: J.F.M.Horne (Kenya)

DUETTING, SOCIALITY AND SPECIATION, WITH REFERENCE TO BARBETS (CAPITONIDAE)

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The studies have focused on the patterns of sociality and group-or pair-duetting in the hole-nesting and roosting African Capitonidae, particularly the genera Trachyphonus and Lybius. These are sedentary species defending territories in pairs or groups year-round in areas where the breeding season is unpredictable. Intricate polyphonic duets with fitted sets of duet songs by the partners in Trachyphonus are correlated with patterns of morphological geographic variation, and with sympatry and allopatry of duetting relatives. Antiphonally duetting species of Lybius show duets to be most different where there is sympatry, and broad sympatry occurs mainly between precisely duetting species and species that either do not duet or have simple simultaneous duet "songs" or calls. Fourteen of 36 African barbets duet; duetters are largely allopatric and seem to differentiate more strongly and perhaps more rapidly speciate than do non-duetters. Duetters are more social, with some cooperative breeding, than are some non-duetting barbets (e.g. Pogoniulus), but less so than other non-duetters such as Gymnobucco sp., Lybius melanopterus, and others. A problem exists

in how different the duet roles may be to preclude interbreeding of duetters. Duetters often have "helpers", which are usually prevented from participating in the duet of the primary pair. At least in Lybius leucocephalus and probably in Trachyphonus darnaudii there can be differences in details of duets among conspecific populations, whereas major differences in timing and structure of duets (e.g. between Trachyphonus erythrocephalus and T.darnaudii,and between Lybius torquatus and L.rubrifacies) seem required for sympatry and the culmination of speciation.

ALLOSPECIATION AND SOCIAL EVOLUTION IN MEROPS (MEROPIDAE) WITH A SYNOPSIS OF CORACIIFORMES
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Merops bullocki and M. bullockoides comprise a classic superspecies, with its two allospecies nearly in contact in the Albertine Rift. Each has been studied demographically; they breed colonially and co-operatively, and there are some minor differences in their social organizations (Nigeria cf. Kenya). These differences are explored but cannot yet be related with any ecological dissimilarities. Natural selection is discussed in relation to body size, sex ratio and survival.

Other Merops species which have been investigated range in social organization from solitary, monogamous forms without helpers (M.pusillus, M. boehmi) through more or less densety aggregated forms with a low (M.apiaster, M.nubicus) or high incidence of helpers (M. bullocki supersp., M.ornatus), to the loosely colonial M. albicollis with up to six helpers at all nests. Such a spectrum in a genus which is otherwise rather uniform both etho-ecologically and morphologically ought to disclose character correlates and hence indicate evolutionary causation. The most promising indication seems to be survival curve shape; but these birds are long-lived, so that demonstrating a relation between helping behaviour and survivorship will necessitate many years further study.

The genus, with 50 taxa in 18 species (3 superspecies and several species-groups are readily identifiable), well exemplifies the process of allospeciation. Its evolution into temperate latitudes has probably promoted sexual dimorphism of plumage but not affected mating systems. In other respects allospeciation within Merops does not differ identifiably from that of less social species.

SPECIATION AND EVOLUTION OF BEHAVIOR IN WEAVERBIRDS (PLOCEIDAE)
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Three populations of Ploceus cucullatus, representing different subspecies in West, Central and South Africa, differed in degree of polygyny and numbers of nests woven by the males, depending on whether or not the male fed the nestlings. There were also differences in protective behavior related to predation pressure. In this species, the male weaves the nest and displays it

to unmated females, who select a mate. Color diffcrences between males of different species are associated with differences in the nest-displays and details of habitat. Young males, who are ignored by the females, spend much of their first two years in the practice of nest-building.

There are many more species of true weavers (Ploceinae),with marked sex dichromatism, than there are species in other subfamilies of Ploceidae which often lack sex dichromatism, suggesting that a greater intensity of sexual selection in the Ploceinac may have led to a higher degree of speciation.

In the Plocepasserinae, Plocepasser mahali, which finds all its food in a small group territory, has small colonics,while Pseudonigrita arnaudi often has larger colonies which share extensive feeding grounds. Multiple factors, operating together, have probably led to the evolution of the huge, compound and communal nest characteristic of  Philetairus socius.

THE CORRELATION OF AND POSSIBLE RELATIONSHIP BETWEEN
DEGREE OF SOCIALITY AND SPECIATION IN NEW WORLD JAYS

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It now seems likely, based on much new but still incomplete information, that a great majority of New World jays, especially Neotropical ones, are to varying degrees communally social breeders. Of the 19 species of the Ornate Line (Cyanocorax, Calocitta, and Cyanocitta) there is some evidence that 12 of these are communal at least in part of their range. Both species of Cyanocitta are considered non-oommunal. Cyanocorax yncas is communal in parts of South America, at least, but apparently non-communal·in Middle and North America. For 6 species, all South America Cyanocorax, there are no satisfactory data. In the Inornate Line (Cyanolyca, Aphelocoma, Gymnorhinus), the 12 species include 5  that are communal breeders, one (A. coerulescens) seemingly being so only in Florida (USA). Of the 8 species of Cyanolyca 6 are essentially unknown in their breeding biology. C. nana is non-communal, breeding in pairs. C. viridicyana is communal at least at one locality in Peru. The recognized subspecies of various species suggest a slow evolutionary rate. But when one regards the various species now recognized as allopatric forms of a few mega- and superspecies, it can be seen that rapid evolution has occurred, resulting in many distinctive but clearly closed related species of distinctive phenotype. Clannishness and sedentary habit associated with communal breeding probably contribute strongly to this effect. Evidence will be presented from studies of the San Blas jay, Cyanocorax sanblasianus.

THE SIGNIFICANCE OF IMPRINTING AND TRADITION IN
THE EVOLUTION OF BIRDS

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Hand-reared European Bullfinches, isolated from conspecifics for the first 6 months of life, can be trained to whistle short folk songs (up to 80 notes)

as result of sexual imprinting to the human keeper. Females, reared under identical conditions, show sexual excitement and copulation responses if the particular folk song is whistled to them after they have reached sexual maturity. Thus, in the sensitive period of juvenile life, not only morphological characters of the species (or foster species) but also its vocalizations are learned and have a crucial influence on the later sexual preferences.

Based on similar imprinting processes, the males of the African Widow Birds (Viduinae) mimic the songs and calls of their particular host species. Experiments in which young widow birds were reared by another (than the natural) host species have shown, that the young males adopt the vocalizations of the experimental host and that the females prefer males which sing this different type of song. This preprogrammed behaviour has resulted in a parallel evolution of hosts and parasites.

Early stages of this historical development are reflected in the adaptation of the Paradise Widow Bird (Steganura paradisaea) to the subspecies formation of its host, the Melba Finch (Pytilia melba).

## EVOLUTION OF GROUP LIFE WITH SPECIAL REFERENCE TO THE ARABIAN BABBLER (TURDOIDES SOUAMICEPS)

Amotz Zahavi

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Babblers are group territory birds. Groups number 2-15 individuals. Usually one pair breeds and the rest of the group, young and adults, help at the nest. Sometimes up to 3 males and 3 females share in reproduction. Staying in the group is the best option for non-breeders to survive and wait for their turn to breed. The breeders benefit from the large group which help them to defend the territory. Group life select for apparent altruistic activities such as allofeeding, sentinel activity, common defence of the territory and the help at the nest. Individuals compete with one another to act as altruists. Dominants tend to interfer especially with the altruistic activities of individuals, which follow them in the dominance hierarchy, but are tolerant to the altruism of lower members in the hierarchy. Neither kin selection nor any form of reciprocal altruism may explain the social adaptations of babblers. The argument that a helper benefits by increasing the size of the group, on which its future breeding success is dependant, is an argument based on group selection. The apparent altruistic adaptations may be interpreted as an investment in the quality of the altruist.

Another set of social adaptations includes contact behavior allopreening and the peculiar morning dance. It is suggested that the bond among group members is strengthened indirectly from these activities by providing information rather than directly from the activities themselves. It will be argued that the problems of group life are not qualitatively different from the problems involved in the evolution of all other social adaptations.

STRUCTURE OF FEATHERS'

Convener: J.Dyck (Denmark), co-convener: P.Stettenhsim (USA)

MOLECULAR MORPHOLOGY OF FEATHERS: AN EXPERIMENTAL APPROACH

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Understanding the molecular organization of morphologically diverse structures presents one of the most challenging aspects of contemporary comparative and analytical biology. Ws havs undertaken investigations of the molecular structure and supramolecular organization of avian epidermal ($\alpha$ -) keratin structures (feathers, down, scale, claw and beak). All structures consist of fibers organized from filamets constructed from a closely related family of proteins. A minimum of structural differences occur among the $\alpha$ -polypeptides. Yet there are vast morphological and functional differences at the phenotypic level. Our work has encompossed the biochemical basis of polypeptide heterogeneity and the process (in vivo and in vitro) of filament formation. Protein production involves a set of repetitive instructions. Fabrication of filamets is an epigenetic process based on physical recognition and precise interactions of polypeptides.

This information can illustrate constraints of design, and the relationships of supramolecular organization to the structure and function of the features involved. In an evolutionary sense, the major structures probably arose rapidly and perhaps included the "invention" of a unique set of proteins. Parallel changes in the genetic programming produced morphological variation with little change in the structural genes. Overall constraints on shape and functional limitations are a result of the nature of the molecules and the ways in which they can interact.

IMPLICATIONS OF STRUCTURAL DIFFERENCES AMONG
DIFFERENTLY COLORED FEATHERS

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Anecdotal evidence (Averill, Condor 25: 57-59, 1923; Barrowclough and Sibley, Auk 97: 881-883, 1980) and recent experimental evidence (Burtt, The behavioral significance of color, Garland STPM Press, 1979) show that melanic feathers are significantly less abraded by airborne particles than non-melanic feathers whereas abrasion-resistance is unaffected by moderate concentrations of carotenoids. In addition to destruction of feathers by particulate abrasion, feathers are scraped and abraded when they rub against one another or against other objects (e.g., bark, stones, leaf litter). Is resistance to scraping across a rough, unyielding surface different from resistance to collision with airborne particles? What of repeated bending? Feathers at the joints and in the wings and tail are subject to frequent flexing. Is resiliance correlated with the presence or absence of certain biochromes? How does the microstructure of differently colored feathers affect resistance to

the mechanical stresses outlined above? How is the microstructure affected by these same mechanical stresses? These questions are addressed by a combination of electron microscopy and stress analysis developed by mechanical engineers. The results are discussed in light of the pattern of color of wood warblers (Parulidae).

FEATHER STRUCTURE AND MAINTENANCE IN RELATION TO
BATHING, SWIMMING, AND DIVING
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The evolution of feathers in birds may be related to the development of homoiothermy, or flying ability, or both. Feathers provide an efficient insulating covering with a very light weight. In addition, they are essential for the excellent aerodynamic properties of wings and tail.

To maintain these insulating and aerodynamic properties bathing in water seems to be indispensable for a large number of bird species. The most important features of this maintenance behaviour will be described. This will be related to the effects of water on the bird's plumage as deduced from experiments with single feathers subjected to controlled water contacts.

Some birds spend a considerable part of their life on or in water. This requires a number of special adaptations in order to maintain insulation and to provide sufficient buoyancy in swimming birds, or to overcome buoyancy in diving birds. In this context attention will be paid to the structural properties of feathers, the role of the oilgland, and the soaking of some feathers in a number of diving birds, as cormorants.

ARCHAEOPTERYX AND THE EVOLUTION OF
FEATHERS: SOME CONSIDERATIONS
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The last ten years have witnessed a renewed interest in the reptile-to-bird evolution and the related question of the evolution from scales to feather. We found it improbable that feathers first evolved to aid reptiles/birds glide between trees. Because if selection had been for gliding, feathers should be horizontally expanded structures, which they are not when studied at the microscopical level. Neither did we find the other existing theories about scale-to-feather evolution logical and convincing, and he proposed a new theory, namely that feathers evolved in order to increase the water-repellency of the surface of the reptile/bird.

S Y M P O S I U M
STRUCTURE AND EVOLUTION OF AVIAN CHROMOSOMES
Convener: Gerald F. Shields, (USA), co-convener: Nina Bulatova (USSR)

Historically the study of bird chromosomes has lagged far behind studies in other vertebrate groups. Bird chromosomes are inherently difficult to

study because of the presence of microchromosomes which are difficult to count and identify. Only about 5% of the 8,900 extant bird species have been studied and most of these have not been done well. Recently, however, there has been an increase in the number of cromosome studies in birds and this symposium is a first attempt to characterize some of these. We are in a transition period wherein recent studies are beginning to employ techniques which result in a more diagnostic description of the karyotype. Such techniques include the use of more reliable tissue culture media, larger sample sizes, and a variety of procedures used to differentially characterize individual chromosomes.

### KARYOLOGY AS A TOOL FOR SOLVING TAXONOMIC PROBLEMS IN BIRDS

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Three main problems are hampering the use of karyological data in taxonomy: (1) the rate of karyotypic change during evolution in birds, as in other vertebrate groups, is not.constant, so that degrees of karyotypic similarity or dissimilarity do not necessarily reflect degrees of phylogenetic relationships; (2) most, if not all, of the possible karyotypic changes (rearrangements) can occur in both directions, so that it is often difficult or even impossible to distinguish between plesiomorphic and apopmorphic characteristics; (3) the degree of resolution with which avian chromosomes can be studied at this moment is too low. The few large chromosomes of the average bird karyotype generally do not provide enough information, while the smaller elements and the microchromosomes are too small to allow detailed comparisons.

Recent increase of the karyological data available on birds has shown that avian karyotypes are not as uniform as was formerly believed. Although some groups do display uniform karyotypes,others exhibit wide karyotypic variability. In the latter groups in particular karyological data may contribute to the solution of taxonomic problems. Examples are given from Ciconiiformes, Galliformes, Falconiformes and Psittaciformes. In conclusion it may be stated that promising results are to be expected if methods are improved and the karyological inventory of the various avian orders is regourously increased.

### KARYOSYSTEMATICS IN SOME PALAEARCTIC PASSERINES
### (PARIDAE, PLOCEIDAE, CORVIDAE)

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Karyotypes and differential staining of chromosomes were studied in 5 species of Parus, 2 of Passer and four of the Corvidae. Birds of these three families share a common karyotype structure, the so-called "basic karyotype". It designates a large group of families which are not distinguished karyologically and which are systematically close to other relatively less represen-

tative groups within the Oscines. This complex of families could be associated with the extensive radiation (speciation) during the evolution of passerine birds. Karyological differentiation of these species occurred by both structural chromosomal reanangements and by interchromosomal variations of a presumably regulation character. Karyotype data contributes significantly to the study of the systematics and hybridization of those well-known examples of Parus major major and P.m.minor and Corvus corone and C.cornix.

## TRENDS IN THE EVOLUTION OF BIRD CHROMOSOMES

Gerald F. Shields
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Avian cytogenetic research has, until recently, lagged far behind efforts in other vertebrate groups. Avian chromosomes are inherently difficult to study because most exist as minute microchromosomes whose morphology and number are obscure. Since 1966, improvements in methods of culturing avian cells have resulted in an increasing number of comparative chromosome studies whose quality parallels those for mammals.

This recent synthesis in comparative avian cytogenetics now allows us to assess such factors as the overall karyotypic variability in birds and to consider the role that chromosomal change plays in avian speciation. In the present study, chromosomal variability was assessed within and between species of the same genus and within orders of birds. Chromosomal differences among local populations appear to be associated either with mechanisms that support balanced polymorphism or frequency dependent selection and not with speciation. The data are discussed in light of current models of chromosome evolution proposed for vertebrates other than birds.

## CHROMOSOMAL EVOLUTION OF SOUTH AMERICAN COLUMBIFORMES[*]

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Karyotypes of 13 species of Brazilian Columbiformes were compared by conventional homogeneous as well as Giemsa (G) and (C) constitutive heterochromatin staining of chromosomes. Chromosomal rearrangements as evidenced by measurements of arm ratios, relative chromosome lengths and banding patterns appeared more frequent in some pairs. Chromosomes 3, 4, and 5 appeared stable.

The types of chromosomal rearrangements appeared to vary among the genera. The genus Columba was characterized by paracentric inversions, Uropelia and Claravis by chromosomal fusions and translocations and Geotrygon by centric fission. Finally, the genera Columbina, Leptotila, Zenaida and Scardafella were characterized by several rearrangement types including: chromosomal translocations as well as paracentric and pericentric inversions.

All species of Columbiformes thus far studied share a large positive G-band on the first chromosome. The W chromosome is largely heterochromatic while slight heterochromatin exists at centromeric regions on the other chromosomes. The distribution of this heterochromatin was, however, heterogeneous.

Decreases in the size of heterochromatin blocks appeared to be accompanied by increases in G band number in some chromosomes. This suggests a dispersion of heterochromatin into intersticial portions of the chromosomes and this may be based upon rearrangements in internal chromosome regions.

Some modifications and additions of the Columbiform phylogenetic tree are suggested.

S Y M P O S I U M

## STATUS OF THE WORLD'S CRANE SPECIES

Convener: J.C.Lewis (USA), co-convener: I.A.Neufeldt (USSR)

The symposium began with introductory remarks by J.C.Lewis. Ornithologists recognize 15 crane species in the world. The cranes' affinity for wetland habitats, and their preference for isolation from human activities, are disadvantages in a world where wetlands are rapidly being drained or filled and where human populations continue to increase. Several of the crane species and subspecies are rare or endangered. Examples are the Cuban sandhill crane (Grus canadensis nesiotes) of which there are perhaps 200 birds in western Cuba and the Isle of Pines; the Mississippi sandhill crane (G.c.pulla) of 40-50 individuals in Jackson Country, Mississippi, USA: the whooping crane (G.americana) with about 85 wild and 30 captive birds in North America, and the Siberian crane (G.leucogeranus) of 250-310 birds nesting in the USSR. The distribution and population sizes of all crane species are sharply reduced from those of a century ago.

This symposium discussed populations of most crane species; the exceptions were those of Africa and western Europe. The symposium was followed by an evening round table discussion chaired by George Archibald of International Crane Foundation (USA) and Vladimir Flint of the Nature Conservation Research Institute (USSR). The discussion focused on ways to help the endangered Siberian crane.

STATUS OF HOODED AND SIBERIAN WHITE CRANES OF THEIR
WINTERING GROUNDS AND OF BLACK-NECKED CRANES THROUGHOUT
THEIR RANGE

Yi-Ching Ma

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The black-necked crane is the world's only alpine crane species; its nesting areas are 3,500 to 5,000 m above sea level. Even in winter it is unusual for this crane to migrate to warm lowland areas. They have nested in Qinghai and northwestern Sichuan Provinces and southern Xizang Autonomous Region. They used to nest (1930's) in northwestern Kansu Province, but there are no records in recent years. The density of a population nesting at Lonbaotan, southern Qinghai Province, in 1978-79 was 0.76-0.78 cranes/km$^2$ in June. During fall migration this crane is sometimes seen in large flocks. A flock of

300-400 was seen in September 1973 at Tangra Range pass flying southward and in mid-October 1979 a flock of at least 600 was seen in the Tsaidam Basin. Black-necked cranes spend the winter in southwestern Sichuan, southern Xizang, western Guizhou, and Yunnan Provinces. In early December 1979 a wintering flock of 70-80 cranes was found at Caohai in western Guizhou Province where they roosted with G.grus lilfordi. Total populations are unknown but are probably declining due to habitat changes.

The Siberian crane is a migrant and winters in China. In the past, they were recorded nesting around Dalainor and Qiqihar lakes and in Liactung of northeastern China. However, there are no recent nesting records in China. In late May 1981, 24 subadult Siberian cranes stopped near Qiqihar of Heilongjiang Province during migration. Siberian cranes migrate in spring and fall along the Nenjiang River in central Heilongjiang Province and southward along the coastal province to their wintering grounds on the Lower Yangtze River. In January 1981 a wintering flock of more than 100 Siberian cranes was west of Poyang Lake, northwest Jiangxi Province. A winter flock was also reported from the Anquing district of Anhui Province.


## THE STATUS OF RED-CROWNED AND WHITE-NAPED CRANE

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There are two populations of red-crowned crane, a sedentary one in Japan and a migratory one breeding along the middle Amur River and its branches. G.vipio mainly nests in northeastern China and winters in Korea, Japan, and eastern China. Populations of both species in Japan decreased until the end of the 19th Century, and populations on the mainland apparently also greatly diminished during and after World War II. Crane populations have gradually recovered in Japan since the 1950's due to protection and winter feeding programs. In Japan there are now about 250 G.japonensis and over 1,000 G.vipio. Based on recent surveys of japonensis in the USSR and China, populations in the mainland are estimated at 1,000. Two thousand G.vipio have wintered in South Korea recently, consequently the total population may be 3,000-5,000 including those flocks that migrate to eastern China. The red-crowned and white-naped cranes are legally protected, but their nesting habitats are threatened by land development for agriculture and industry, and by construction of roads and railways. On the wintering grounds in Japan there are excess concentrations of these cranes that have led to crop damage on nearby farmlands.


## STATUS OF BROLGA AND SARUS CRANES

P.Gole
World Wildlife Fund representative, India

The western sarus (G. antigone antigone) is restricted to north and central India. Occasionally it has appeared in Kashmir in the foothills of the Himalayas up to 1800 m, and in Sind in Pakistan. The eastern sarus (G.a.sharpii) occurs in India from Assam east to Kamrup and Manipur. Outside India it is reported from Burma, Cambodia, Laos, South Viet Nam, north Malaysia, and the Philippines. But most of the reports are from the 1930's and 1940's.

Since then the reports indicate the eastern sarus has severely declined over most of its range. In the 1960's it appeared in north Australia. The brolga (G.rubicundus) is restricted to Australia. A population estimate is unavailable for any of these three species.

The population of western sarus, according to knowledgeable Indian ornithologists, is either stable or has slightly declined over much of its range. The western sarus has lost nesting and wintering habitat due to human settlement and cultivation. The eastern sarus, the most threatened of the three, appears to have disappeared from the Philippines, Malaysia, and Thailand, and its existence in South Viet Nam, Cambodia, and Laos is doubtful. Its status in eastern India and Burma needs to be thoroughly investigated. In Australia the species appears to be stable or possibly increasing. In mainland Asia the decline seems due to hunting and loss of habitat. In Burma and the Philippines, the destruction of tall grass habitat probably caused its decline. The main threat to the brolga appears to be destruction of habitat.

STATE OF BREEDING POPULATIONS OF COMMON, ASIATIC WHITE,
HOODED AND DEMOISELLE CRANES IN THE USSR
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Siberian Crane (Grus leucogeranus). In the USSR there are two separate populations: West-Siberian and Yakutian. West-Siberian population nests along the right tributaries of the Ob River to the north of Beryozovo town (in 1981 8 nests were found in the Kunovat River Valley). Overall numbers don't exceed 50-60 birds and are likely to reduce. Yakutian population breeds on a stretch of flat marshy tundra between the Yana and the Kolyma Rivers (the bulk of population nests between the Indigirka and the Khroma rivers). The numbers are 200-250 individuals (about 60 breeding pairs) and remain comparatively stable.

Common Crane (G.grus). Overall numbers are unknown, but according to indirect data they comprise 60-100 thousand individuals. The numbers reduce over the whole territory of the European part of the USSR (except some boreal forest regions), because of bog degradation. In Western Siberia the numbers are relatively stable (in Baraba Steppe the density is 0.5-9.2 individuals per 100 $km^2$). In Kazakhstan and eastwards the numbers reduce.

Hooded Crane (G.monacha). Overall numbers within the breeding range are unknown (according to count data obtained at wintering places in Japan in 1981 the population was more than 4000 individuals and even increased). The condition of nesting habitat (almost inaccessible moss-larch bogs of middle and southern taiga situated in the south of the Middle-Siberian Plateau, in the lower and probably middle Amur basin) is satisfactory. The largest of all known colonies is situated in the lower Bikin River (about 50 pairs, two thirds of which do breed; nesting density is about 1 pair per 20-25 $km^2$).

Demoisalle Crane (Anthropoides virgo). According to the indirect data overall numbers comprise 45-50 thousand individuals. High density was observed in some regions of Pricaspian Lowland (up to 42 individuals per 100 $km^2$), in Western and Central Kazakhstan, the Altai, the Tuva and in the southern

regions beyond Lake Baikal. Over the remaining portions of the breeding range the numbers considerably reduced in seventies, although during several last years certain stabilization is being observed. It is the consequence of changing the nesting habitat by breeding pairs by shifting their breeding territories from ploughed steppes southwards to the zone of arid semi-deserts (changes in range outlines) and use of man-made landscapes to some extent (nesting on sowing areas).

STATUS AND DISTRIBUTION OF CRANES IN NORTH AMERICA
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The whooping crane reached a population low of 21 in 1941 but now numbers about 85 wild and 30 in captivity. This bird is symbolic of United States of America efforts to conserve endangered species. The only self-sustaining population winters at Aransas National Wildlife Refuge and vicinity on the Texas Gulf Coast and nests in Wood Buffalo National Park, in northern Canada. A unique restoration experiment is underway to establish a second wild population that will nest at Grays Lake in Idaho and winter in New Mexico.

There are six sandhill crane subspecies (G.canadensis): three are migratory. Nonmigratory subspecies are the Cuban (G.c. nesiotes) which is believed to number about 200 living in western Cuba and on the Isle of Pines, the estimated 6.000 Florida sandhill (G.c.pratensis) of Florida and southern Georgia, and the 40 Mississippi sandhills (G.c.pulla) of Jackson County, Mississippi. An estimated 40.000 to 45.000 greater sandhill cranes (G.c.tabida) nest in the northern United States and winter in the southern states. The Canadian sandhill crane (G.c.rowani) nests in central Canada, winters in Texas, and totals about 55.000 birds. The lesser sandhill (G.c.canadensis) crane which nests in Siberia, Alaska, and northern Canada, winters in Texas, New Mexico, California, and Mexico, and totals over 500.000 birds. The lesser and Canadian races are hunted in parts of North America and the annual harvest is close to 20.000 birds.

Four Russian scientists (A.A.Vasilchenko of Sohonda Reserve, Yu.V.Shibaev and N.M.Litvinenko of the Institute of Biology and Soil Sciences in Vladivostok, and S.M.Smirensky of Moscow State University) presented brief unscheduled reports on the status of rare cranes in specific parts of the USSR.

S Y M P O S I U M
PHYSIOLOGY AND ECOLOGY OF INCUBATION
Convener: S.Haftorn (Norway), co-convener: H.Biebach (FRG)

THE ASSESSMENT OF THE ENERGY REQUIREMENTS FOR INCUBATION
Joseph A.L. Mertens
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Efforts made during the past decade to assess the energy requirements of birds for incubation have produced conflicting results.

Computations based on heat-budget modeling predicted that a bird might accomplish the incubation without increasing its heat production about the level of the resting metabolic rate.

However, recent direct measurements on incubating Great Tits showed a considerable increase of the nocturnal heat production during the transition phase from egg-laying to incubation and the birds continued this high level of heat production throughout the whole incubation period. The question will be discussed of why birds obviously spend more energy for incubation that should be sufficient on the basis of computations.

TYPES OF HATCHING AND HETEROGENEITY OF BIRDS
EMBRYOS DEVELOPMENT

A.I.Shurakov, A.M.Bolotnikov
Perm Pedagogical Institute,USSR

In the process of evolution of birds 3 types of hatching arised during oviposition (relatively uninterrupted, interrupted and combined) - A.M.Bolotnikov, A.I.Shurakov, 1970, - which in a compound complex of behaviour reactions are nothing but taking care of posterity, directed to the full realization of primary fecundity.

The combination of heatings of eggs in periods of visiting a nest by a brood-hen with hindering the development of embryos, while she is absent, during graduate increasing of density of hatching (the 2-nd and 3-rd types) and graduate raising inside nest temperature under the influence of a stage of a hatching spot's development (all types) conditions the difference in the speed of development of every oviposition from the very beginning (established on 88 speices of birds, 13 orders and 31 families).

Heterogenety of the development arising during ovioposition is preserved in the embryo and post-natal onthogenesis, it is the common regularity for the class of birds and is considered to be one of the mechanisms of the appearance of phenotypical heterogeneity individuals of each brood, and therefore population on the whole (heterogeneity of broods in population increases at the expense of stetching out of nesting).

THE PHYSIOLOGY OF INCUBATION AND ITS IMPLICATIONS
ON CHICK SURVIVAL

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Aspects of incubation have been studied in the domestic hen and in the willow ptarmigan (Lagopus lagopus) both in the laboratory and in the field. The female incubates alone and leaves the nest one to three times a day to forage. During her absence the eggs cool off. The degree of cooling depends on the ambient weather conditions and on the duration of her absence. Upon return the female increases her metabolism and heart rate to rewarm her eggs. The degree of metabolic increase depends on the temperature of the eggs. At 5°C egg temperature, the female will increase the metabolism three to five times, the metabolism tapering off as the eggs become warmer. In a ptarmigan hen the caloric cost of rewarming 10 eggs from 10-40°C requires an $O_2$ consump-

tion of 1500 ml $O_2$/hr compared to a resting metabolism of 375 ml $O_2$/hr. The energy required for re-warming must be secured during the foraging intervals. Field studies indicate that poor weather conditions may lead to negative energy balance thus rendering the hen in poor condition at hatching. Accurate control of water loss from the eggs during incubation affects the vitality of the chick. Preliminary data on ptarmigan chicks indicate that this may be a factor in annual chick production.

THE ENERGETICS OF INCUBATION IN STARLINGS (STURNUS VULGARIS)
AND POSSIBLE ECOLOGICAL CONSEQUENCES

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During incubation by female European Starlings the potential time for foraging is greatly reduced because they spend most of the time on the eggs. Together with the added energetic cost of incubation this phase of the breeding cycle might be the energetic bottleneck for reproduction. Direct measurements of energy expenditure during steady state incubation at night and in the day, and during rewarming of the eggs after an inattentive period allow predictions of the total energy budget. An earlier than normal onset of incubation should result in a negative energy balance, and this effect is increased by an increase in clutch size. The length and amount of inattentive periods are important for energy balance because of the great amount of energy needed for rewarming the eggs.

. S Y M P O S I U M
MOULT
Convener: E.Sutter (Switzerland), co-convener: C.Edelstam (Sweden)

MOULT IN LARGE RAPTORS

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Traditionally, the study of moult rests on the examination of actively moulting birds. Large raptors in active moult are rare in collections, and few are trapped and examined alive. Moreover, analysis becomes complicated in this case by the fact that individual wing quills may serve their owner for two years or more, and three or four generations of flight feathers may be present at any one time.

By recording carefully the state of wear and fading of every quill in a large number of postjuvenile specimens, whether actively moulting or not, it is possible to reconstruct the details and time schedule of this moult process. In the course of the present study, notes were taken of the status of over 50 000 quills in more than twenty species. The moult pattern was found to be serially continuous. A key to the determination of age of the immature bird is provided by the regular generation (once a year, in the species so far examined) of a new moult wave among the inner primaries. This in turn offers an opportunity to study the temporal development of plumage,

and thus to obtain more reliable age criteria than have hitherto been available for most large raptors.

The use of such criteria will be demonstrated by a series of slides of eagles photographed in the field.

In serial moult (Staffelmauser) in Falconiformes the flight-feathers, primaries and secondaries, are replaced in regular sequence, starting from several centres. The primaries have a single centre at the carpal joint. The innermost primary (nr 1) is the first one to be replaced in every single moult-wave. However, in contrast to the situation in smaller species (e.g. Accipiter nisus) the replacement of a set of primaries is not completed in the course of one season in larger species (e.g. Pandion, Haliaeetus, Segittarius, Vultur). So in first-year birds of these species the juvenile outer primaries are retained. In the next moulting season the moult is resumed where it was suspended, but also a new moult wave is started at primary 1. As the birds grow older, three or more series may be active at the same time. This slow type of moult assures that the wings always retain a rather closed surface without big gaps.

PRIMARY MOULT STRATEGIES IN TERNS STERNIDAE
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In 1966, Stresemann and Stresemann (J. Orn. 106, Sonderheft) established the existence of what they called Staffelmauser or serial moult. It was supposed to occur mainly in tropical species of Galliformes, Columbiformes, Caprimulgiformes, and Bucerotidae, but also in Pelecaniformes of both tropical and temperate regions. Most of these species moult is serially descendant, and in recent years such a serial descendant moult is widely established in members of Ciconiiformes, Accipitridae, Otididae, Strigiformes, etc., especially in larger and slow-moulting species, but also in some Charadriiformes with limited time available for moult. Rather different from this serial descendant moult is that of most Sternidae: at the end of the nesting season, primary moult starts descendantly with the innermost; when this series is about half-way, a 2nd series starts, again with the innermost, while in smaller terns (dougallii, Gygis, some Chlidonias, albifrons and relatives) even a 3rd series may start in the same moult season. At the end of this season, feather replacement halts, and, unlike normal Staffelmauser, is not resumed in the next season. As a result, outer primaries are replaced once a year and innermost 2-3 times a year, although the latter wear much less quickly. That not abrasion necessitates such a surplus replacement may be seen from some species like Sterna paradisaea, fuscata, and anaethetus with relatives, which with a similar way of life show a single series per season only.

It seems a vaste of energy to replace the inner primaries three times during the course of a single year. After considering several possible explanations, Mr. Roselaar concluded that it may be important for terns to have in spring freshly moulted white inner wings as these are shown to the partner during sexual display. When the feathers are worn, they quickly become grey to dark grey. Repeated renewal would prevent the wing from becoming dark. In
1054

black-winged terns, such as <u>Sterna fuscata</u>, no serial moult is present, whereas in <u>Chlidonias niger</u> it is much reduced in comparison with <u>C.hybrida</u>. <u>Sterna paradisaea</u> also lacks the serial moult, but this is related to its extensive migrations and short moulting season in the southern oceans. In the discussion the point was raised the serial moult might not be present in all populations of a species, as students of <u>Sterna antillarum</u> had not found it in birds of the American west coast.

## SHEDDING INTERVALS OF THE PRIMARIES DURING
## POSTJUVENAL MOULT OF THE TREE SPARROW <u>PASSER MONTANUS</u>

E.Sutter
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The Tree Sparrow has a complete moult of the juvenal plumage in autumn. As three broods are raised during the breeding season, there are three groups of young with different fledging dates, different dates of the beginning of moult and even differently scheduled moult. Young of first broods started moulting at the age of 45 days, whereas young of later broods started at 31-34 days of age and moulted faster. In late moulting birds feathers were shed at markedly shorter intervals than in the young of the first brood: The shedding intervals decreased with season. However, this trend was restricted to the innermost primaries and there was a strong tendency to retain the longer shedding intervals in the outer wing, even late in the season. The occurrence of maximum shedding intervals between outer primaries seems to be characteristic for a great variety of bird species. Such a pattern might be related (1) to the prolonged growth period of the outer primaries and (2) to the maintenance of an efficient flying capacity during moult.

## THE RELEVANCE OF MOULT STUDIES FOR TAXONOMY

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Although moult is of limited use in evaluating relationships, it may be used in two other ways. (1) Discriminating between age-classes and sexes in a population, as was shown for big raptors. (2) Separating populations or subspecies on the basis of their moulting schedules. Looking at the relation between moult studies and taxonomy from another side it is clear that in assigning a number of species to the same order, family or genus implies that these species are similar in many respects. When one has worked out the peculiarities of the moult in one species of a group, it is often very much easier to interpret the findings in other species of the same group. More important, however, is the function of drawing attention to peculiarities which may be explained in terms of different ecology or ethology. The moult of <u>Sterna paradisaea</u> is a case in point. When we know that the terns all have a special type of serial moult as was described by Mr Roselaar the "normal" descendant moult of this species asks for explanation. On the other hand and on a wider scale, when we know that gulls (<u>Laridae</u>) and skuas(<u>Stercorariidae</u>) have a regular descendant moult, it is the serial moult of terns that invites us to propose explanatory hypotheses. This function of taxonomy

is not very obvious, because we are so accustomed to think in this way, but it is no less real and often forms the unthought-of foundation of all work in ornithology.

SYMPOSIUM
SONG DEVELOPMENT AND SPECIES EVOLUTION
Convener: J.Martens (FRG), co-convener: J.C.Bremond (France)

SOCIAL INTERACTION, SENSITIVE PHASES AND THE SONG TEMPLATE
Luis F. Baptista California Academy of Sciences, California 94118, USA

The literature indicates that tape tutored White-crowned Sparrows (Zonotrichia leucophrys) learn songs between 10 and 50 days, prior to dispersal from their natal area (at between 35 and 48 days). A stimulus filtering mechanism also directs naive individuals to select conspecific and reject allospecific songs as models for imitation.

Fifty day old White-crowned Sparrows placed in special double-compartment cages wherein each experimental could see and hear one living conspecific tutor successfully learned its song and ignored all other songs it could hear in the room. Some experimentals successfully learned the songs of Strawberry Finches (Amandava amandava) when the latter served as tutors. Controls raised in anechoic boxes sang simplified Kasper Hauser songs. It is postulated that social interaction with living tutors extends the sensitive phase for song learning beyond the fifty days established by using tape tutors. Additionally, social interaction with live alien tutors overrides the innate preference for conspecific songs, so that experimentals chose alien songs as models for imitation.

Two popular theories as to the adaptive significance of learning a dialect occur in the literature. One theory, the assortative mating theory, suggests that females selectively mate with males singing their own dialect to promote some inbreeding and fixate adaptive genes within a habitat. Songs from female White-crowned Sparrows induced with testosterone seldom matched the dialects of their mates, casting doubt on the validity of the assortative mating theory. A second theory, the social adaptation theory, suggest that males learn songs of residents at sites settled, because matching their song gives them some social advantage in gaining and holding a territory. Songs of nearest neighbors in natural populations of White-crowned Sparrows are more similar to each other than to songs of non-neighbors. This could be due to birds learning songs directly from their fathers and settling nearby, or due to young birds coming in and matching songs of local studs. Studies revealed that few males banded as nestlings settled near their place of birth, and few birds matched songs of their fathers. Since our laboratory studies indicate that birds may learn songs beyond 50 days, and thus after dispersal from their natal area, the likely explanation for the clumped distribution of song types in the wild is that young males match songs of territory holders at sites settled. These data lend support to the social adaptation theory to explain the adaptive significance of song learning in White-crowned Sparrows.

1056

INFLUENCES OF NATURAL SELECTION AND WITHDRAWAL OF
LEARNING ON SONG OF OSCINES
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The song of oscines has been and still is influenced by various factors.
Body size, structure of sense-organs as well as the habitat where the birds
are living have determined mainly the pitch of their own voices, i.e. some
kind of skeleton conditions. On the other hand, the structure of song notes
is principally a product of learning.

Wild Short-toed Treecreepers (Certhia brachydactyla), for instance, sing
rather uniform, whereas ♂♂ hand-reared separately in laboratory all sing
different to wild ones. Moreover, each separately hand-reared ♂ sings dif-
ferent to all other hand-reared ones. Thus the song of oscines can alter
significantly from one generation to the next by withdrawal of learning. In
this way, something entirely new is introduced into evolution: The possibi-
lity of sudden alteration of a signal. Evidence for tradition of such a
drastically altered signal has been produced in experiment on Short-toed
Treecreepers: Hand-reared young birds imitate the song of hand-reared adults.

The author having investigated more closely the case of Chiffchaff (Phyl-
loscopus collybita), a small Warbler of about 8 to 9 g of weight, it may well
be demonstrated that withdrawal of learning might be the cause for geogra-
phically divergent song structures. Chiffchaff ♂♂ sing rather uniform in
wide regions of Europe and Iran whereas in Spain they sing thoroughly dif-
ferent to all other in Europe.

Chiffchaff ♂♂ from Middle Europe hand-reared in sound proof rooms sing
entirely different to wild ones and similar to Spanish ones. This infers the
hypothesis: Young Chiffchaff ♂♂ of the Middle European song structure have
populated Spain before having learnt their own song structure. Their song
thus became different to that in Middle Europe. The young of those birds
again learned their sires' song, thus creating a new tradition having been
carried on up to this day.

There are other hypotheses explaining the song differences between Spanish
and Middle European song structures by loss of contrast when no closely re-
lated species are to be found in Spain, or by accentuation of contrast when
closely related species are existing in other parts of Europe. Finally, there
might be a connection between song differences and different kinds of habit-
ats. Most arguments, however, tell in favor of the hypothesis of withdrawal
of learning.

CULTURAL EVOLUTION AND MACROGEOGRAPHIC VARIATION
IN SONG PATTERNS
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Unlike morphological or biochemical traits, bird song patterns are often
acquired by imitative learning. Once a species has evolved the capacity for
vocal imitation, its songs are subject to cultural evolution. Two lines of

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evidence were used to assess the effects and importance of cultural evolution on geographic variation in avian song patterns.

An In-depth Analysis of One Species. In 1940 a small population of wild-caught House Finches (Carpodacus mexicanus) native to western North America were introduced onto western Long Island, New York. That introduction initiated an ideal evolutionary experiment: it was recent; it occurred only once and in one, restricted, extra-limital location; and the history of subsequent colonization and spread in eastern U.S.A. is well documented. Song variation was determined by sampling modern populations that now inhabit the entire extent of Long Island. Geographic variation was analyzed graphically with isoglosses, a technique borrowed from human dialect geography. An isogloss is a line that maps the geographic distribution of a given vocal variant. Several isoglosses may run along in parallel forming bundles which mark the boundaries between vocal traditions. Two types of House Finch boundaries were identified: 1) song dialect boundaries, and 2) song institution boundaries. Song dialects are local pronunciation variants, i.e., different local populations pronounce the same basic set of syllable types differently. The song institution in a new concept. It is regional rather than local in extent, and is based on differences in song syllable vocabularies. Different song institutions are characterized by qualitatively different lexicons (syllable repertoires) just as different human languages are. There are over two dozen modern House Finch song institutions on Long Island as compared to only three or four likely for the original founder colonies. The evolution of over twenty new sets of song syllables in less than 30 years is too rapid for biological evolution alone, but it is readily accounted for by cultural evolution. Overall, the House Finch is a songbird in which different regional populations are characterized by qualitatively different syllable repertoires, and the striking differences among these syllable sets are primarily the result of cultural evolution.

Inter-specific Comparisons. A comparison of 27 passerines whose song variation was sampled regionally suggested that each species has its own species-typical song development program, and that the importance of cultural evolution on song variation varies significantly among species. The majority of species in this sample (18 species) had qualitatively different song syllable repertoires in different regions. Like the House Finch, cultural evolution may play an important role in the song variation of such species. A sizable minority (8 species) were characterized by vocal imitation and by each having only one basic syllable repertoire throughout its regional sample. Song variation in such species was interpreted as the product of both a constrained cultural evolution and to strong species-typical constraints on song development. Finally, one species exhibited species-typical constraints too but also very little evidence of vocal imitation. Cultural evolution may have little or no effect on song variation in species with such a song development program.

# GEOGRAPHIC SONG VARIATION, INTERSPECIFIC RESPONSE
## TO SONG AND SONG DEVELOPMENT IN REGULUS

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According to various authors, the genus Regulus consists of at least 4 species. Above all, vocalizations and behaviour of the two European species, Goldcrest (R.regulus) and Firecrest (R.ignicapillus), are well known by studies of THALER, LÖHRL & THALER, LEISLER & THALER, BECKER and others. In regard of behaviour, Goldcrest and Firecrest show greatest interspecific differentiation in vocalizations.

In this paper, refering mainly to my studies of vocalizations of these two European sibling species, some aspects are picked out contributing to the subject of this symposium.

Vocalizations and their discrimination. In Goldcrest and Firecrest, vocalizations are significant of interspecific behaviour and serve as isolating mechanisms. ♂♂ distinguish their species-specific vocalizations from those of the sibling species (as playback experiments revealed), and territories normally overlap.

Geographic variation in song. We find uniformity in the continuous area of Central Europe but great interpopulational differences in western and southern Europe, mainly Spain, inhabited by isolated populations. Thus development of dialects accompanies the separation of populations which is believed to be one of the main preconditions for speciation.

Responsiveness to other dialects declines with decreasing structural similarity of test song to that of the local population. Therefore, individuals from populations characterized by different dialects can experience problems in communication, though these apparently can be overcome through calls, common and widespread song parts and through learning as mixed-dialects-singers show. From these findings it remains questionable if in Goldcrests dialects can build up a barrier against interpopulational exchange in birds; yet they appear to represent first steps toward song in its function as an isolating mechanism.

Character displacement. It is not found in sympatric populations. As allopatric Firecrests react stronger to Goldcrest songs than sympatric ones, the contrast between species' song partly has to be learned by Firecrests in sympatry.

Songs and co-existence. Individual experience, being significant for interspecific response, can also be seen in specimens singing mixed songs and in interspecific territoriality. Both occur only exceptionally in the species with much lower population density locally, presumably caused by "incorrect" imprinting. Thus the isolating mechanism song, built up through learning, can become lost secondarily by learning in special conditions, often near the border of a species' area. Loss of isolating mechanisms facilitates hybridization which can occur successfully in the two species under consideration.

Song development in the genus Regulus. According to our knowledge derived from comparison of songs of all species and many subspecies and populations, songs in Regulus consist of two parts, the main part and a variable ending,

with the exception of <u>R.ignicapillus</u> and presumably populations of <u>R.regulus</u> <u>japonensis</u> living in the Ussury region in East Siberia. In both cases, the song ending was obviously lost during evolution.

S Y M P O S I U M
<u>ADAPTATION TO DESERT CONDITIONS</u>
Convener: I.C.R.Rowley (Australia), co-convener: N.N.Drozdov (USSR)

NOMADISM AS A RESPONSE TO DESERT CONDITIONS
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All birds have the problem of finding resources on which to sustain life from day to day. In arid lands those needed by some species may occur infrequently at one site so that the bird often has to move long distances once a site is exhausted before it finds another where its requirements are met. Usually the direction of movement must differ every time the bird has to move. It is not clear how a bird finds these resources, but it is clear that it depends for survival on finding at least adequate food and that in arid lands the occurrence of this year by year is less predictable than in higher rainfall areas. Every such episode has three elements, initiation, orientation and termination that can be recognised in the behaviour of each individual in a population undertaking a movement. The movement pattern shown by the population as a whole is the result of the behaviour of the individuals within it. A characteristic of some arid zone species is that not all individuals initiate at the same time, orientate in the same direction or terminate at the same  place. Some, often many, individuals will not survive, but so long as some do the population will be preserved. Provided that those which survive are not always those that move at the same time in the same direction to the same place, the movement is not a migration and the species can properly be called nomadic. A proportion of birds living in arid areas exhibit nomadic behaviour, and those that do depend upon resources whose distribution is unpredictable. Many other species are successful residents because their needs are met regularly in the same place, even in arid areas.

ON SOME ADAPTATIONS OF BIRDS DUE TO THE ANTHROPOGENIC
EFFECTS ON THE KARA-KUM DESERT
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Some ecological and ethological adaptations are discussed that originate in typical arid and intrazonal bird species as a result of the economic development of the desert. <u>Buteo rufinus</u>, <u>Lanius excubitor</u>, <u>Scotocerca in-</u><u>quieta</u>, <u>Passer simplex</u> and others change the positions and heights of nests in areas with degraded woody-shrub vegetation. The anthropogenic effect on <u>Passer simplex</u>, that is closely related to sand acacia (<u>Ammodendron conollyi</u>) ecologically, can be both adverse (nesting sites decrease due to anihilation of sand acacia) and favourable (nesting sites increase due to extension of

areas with sand acacia). Not only Buteo rufinus, Cerchneis tinnunculus and Athene noctua, but also such species as Burhinus oedicnemus, Passer simplex, Podoces panderi and Corvus ruficollis which are narrowly specialized in nest respect, change their nest stereotype and place their nests on components of the anthropogenic landscape that arose in the desert, with some of them being observed to have increased fecundity (e.g.,Athene noctua has up to 12 eggs here instead of 5 to 7, Buteo rufinus has 6 instead of 3 to 5, etc.). Because of the scarcity of sites for nesting, birds are forced to nestle in unusual conditions, e.g., Upupa epops, Passer ammodendri and Passer indicus - in the casing and pipes of an unused water-raiser, and Scotocerca inquieta - in a tin. Ecologically pliable birds, such as Streptopelia senegalensis, Acridotheres tristis, Pica pica and others, penetrate far into the desert following man, often as far as 150 to 200 km from the nearest oases.

The facts described cannot be attributed to some anomalies of the ecology and behaviour, but should be regarded as manifestations of the adaptation aimed at conservation of the species under the extreme conditions of the desert.


ENERGETICS, THERMOREGULATION, AND WATER BALANCE
OF DESERT BIRDS

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Deserts are areas of intermittent and generally low productivity. Birds occupying or passing through them must content with potentially severe problems of energy balance, as well as with the better publicized challenges of temperature regulation and maintenance of water balance under heat and aridity. Avian adaptations involving basal metabolic level or torpor will be considered in relation to these energetic problems.

Thermoregulation in heat can produce substantial loss of water in evaporative colling. This process will be reviewed in combination with a consideration of the importance for the water balance in desert birds of their being able to maintain a controlled hyperthermia in the heat and utilize behavioral patterns that reduce heat stress.

Like birds generally, desert species gain water from their oxidative metabolism and from ingesting it in their food or by drinking. They lose water through evaporation and by voiding urine and feces via the cloaca. The water economies of certain desert birds will be examined and mechanisms that curtail evaporation or cloacal water loss, or facilitate rehydration described. Included in this discussion will be consideration of a few exceptional birds which can subsist under certain conditions on a dry seed diet without drinking.


THE ECOLOGICAL-PHYSIOLOGICAL ADAPTATIONS OF WATER
METABOLISM IN DESERT BIRDS

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A comparative physiological analysis was carried out with twelve bird species of the Southeastern Kara-Kum Desert. Special features of water metabolism

were investigated in birds living under different ecological conditions of the arid zone. Some tissues of the birds under investigation consume more water than others depending on the physiological state of organism. Ecologically different groups of birds responded non-uniformly to moisture decrease in food in the experiments with dry feeding.

The results of research into electrolyte contents in tissues and organs show that the specific features of their distribution are of great importance to retaining and redistribution of water in bird organisms. In particular, it was established that the desert species are characterized by high concentrations of sodium and potassium in internals and caudal parts of intestines. The level of absorbtion is also intensified by increasing electrolyte concentrations in the walls of caudal sections of intestines, manifested especially clearly with overheating. The content of eleotrolytes (with relatively lesser amount of water in internals) seems to reflect adaptational responses of the desert species to arid conditions.

Kidneys play an important part in the regulation of water-saline homeostasis. Renal losses of water in desert bird species can be reduced to limits ultimately permissible for the organism. The process of intensive reabsorbtion of water in kidney tubules is predetermined largely by structural features of the excretory system. With adaptations to arid conditions, the ability for osmotic concentration of urine in birds, as distinct from mammals, originates due to the development of a complex of structures of kidney medulla, rather than to lengthening of Henle's loops.

THE SANDGROUSE (PTEROCLIDAE): ADAPTATIONS TO THE
DESERT ENVIRONMENT
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Sandgrouse (Syrrhaptes, 2 spp.; Pterocles, 13 spp.) live in Afro-Asian deserts where they may experience high temperatures and heat loads or low temperatures and heat losses, depending on locality and season. Being small (150-450 g) and ground-living, they have an adverse (surface/volume) ratio, but live in the habitat zone of thermal extremes. In Pterocles spp., insulation is increased at both high and low ambient temperatures, by raising feathers and huddling together with other inidividuals. Radiant heat exchange is regulated by seeking sun or shade, as appropriate. Resting metabolic rates are apparently low, and metabolic heat production is minimised under hot conditions by reducing activity; this effect is more marked in dehydrated than hydrated birds, and very marked in incubating birds which normally sit in full sunlight. Convective heat loss may be exploited under hot conditions, but is not always appropriate, and some species use forced evaporation for heat dispersal only as a last resort. Water turnover is low (3-4% body wt.day$^{-1}$), and individuals may drink only every 3-5d, saving energy by infrequent flights to distant drinking places, and reducing exposure to predators which congregate there. Birds feed selectively on seeds high in protein and energy, but differential feeding techniques in sympatric species suggest that interspecific competition for food is avoided.

## THE LEVELS AND ASPECTS OF CONVERGENT ADAPTATIONS
## IN DESERT BIRDS

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Adaptations of organisms to analogous environmental conditions in the process of evolution lead to convergence (approximation of features). This is manifested especially vividly under extreme conditions, and under arid conditions in particular, as many factors of the environment here are within the sphere of a minimum or a maximum and require of living organisms intricate adaptations, often on the verge of their biological possibilities. The phenomenon of convergence is traced clearly in a comparative analysis of organisms of isolated arid regions with fauna differing in composition and scarcely related, but with analogous ecological conditions. Such an analysis of individual bird species and communities in separate aridity centres of the Earth gives ample material to reveal convergent adaptations at different levels and in different aspects. Two levels of adaptations are singled out in the process of evolutionary convergence, viz. adaptations at a level of species and at a level of communities. Four main aspects of convergent adaptations are distinguished at a level of species, namely, morphological, physiological, ecological and ethological aspects. The degree of convergence at a level of species is determined by a collection of aspects in the pair of species under research and by the extent of their taxonomic chyatus (appertaining to various species, genera or families). The degree of convergence at a level of communities can be established by a general similarity of structural-functional models of the biocoenoses under comparison and by a number of analogous blocks formed by the non-related components. The study of convergent adaptations allows distinguishing the trends and evaluating the limits of adaptation evolution of both the birds themselves as a whole and the communities they are part of.


S Y M P O S I U M
## SEABIRDS AND NUTRIENT CYCLES
Convener: J.R.Croxall (UK), co-convener: A.M.Golovkin (USSR)

## SEABIRD METABOLITES: A SPECIAL FORM OF THE RELATIONSHIP
## BETWEEN BIRDS AND MARINE ECOSYSTEMS

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The necessity to consider the role played by seabirds in marine biocenosises is due to their consumption rate and also to the importance of bird metabolites as seawater fertilizers. The latter is insufficiently studied.
The coefficients of metabolism (food/wet weight/: excrements/dry weight/) appear to be the same for different fisheating seabirds (8.2-9.0). In seawater 0.161 mkg at phosphate phosphorus, 0.549 organic phosphorus, 0.036 nitrate

nitrogen and 1.856 organic nitrogen dissolve from 1 mg of bird excrements. Bird droppings add a little to nitrogen and phosphorus concentrations in areas with mean densities of birds. However the excrements do influence the biogenic substances regime in the vicinity of nesting grounds with high bird density. In the North only 8.0-25.7% of excrements are deposited on shore during breeding season. All the rest fertilizs the water mass. Analysis shows that enriched water areas exist near nesting grounds in the Barents, Chukchi, Okhotsk, Caspian and Scotia Seas. They were confirmed mathematicaly as hydrochemical anomalies. The size of the areas (2-240 km$^2$) depends on the number of breeding birds. The seabirds involved in circulation of organic matter near seashore account for the rate of circulation, redistribution of substances, local phyto- and zooplankton productivity and stability. These areas are typical of marine ecosystems. They were discovered not only near bird colonies but in the vicinity of coral reefs, mussel grounds, etc. The relationship between seabirds and marine ecosystems, through metabolites is of great importance. It confirms a seabird being a genuine marine organism.

TROPHIC DEMANDS OF SEABIRDS IN ALASKAN WATERS

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Trophic demands of seabirds were estimated for the shelf waters of the southeastern Bering Sea distant from colonies, for waters adjacent to the Pribilof Islands in the Bering Sea, and in the vicinity of Kodiak Island, in the western Gulf of Alaska. In the open southeastern Bering Sea, trophic demand varied between oceanographic domains, as defined by water column structure. For depths of less than 50 m, the uniformly mixed waters of the inner domain supported heavy trophic demands by shearwaters. The middle domain, of 50-100 m depth characterized by a two-layer water column, supported relatively few birds. The outer and shelf edge domains (100-200 m depth) supported large numbers of birds, with 1-2% of the primary productivity cycling through seabirds. In the Gulf of Alaska as a whole, trophic demands varied seasonally, largely due to the movements of shearwaters, which accounted for as much as 92% of the total energy flow through the bird community.

Nearer to breeding colonies, trophic demands were more concentrated spatially and were generally of greater magnitude. In the vicinity of the Pribilof Islands, seabird populations were large, with mean densities of up to 530 birds per km$^2$. Trophic dsmand there showed a strong seasonality associated with brseding activites. Murres (Uria) aooount-ed for roughly 80% of the aggregate avian community trophic demand, and their foraging activities were concentrated in areas within 40 km of the breeding colonies. Including the additional demands of chicks, the trophic demand near the Pribilof Island colonies was more than an order of magnitude greater than that in the outer domain, and showed quite different seasonal patterns. Estimates of trophic demands of the dominant breeding seabirds in colonies on Kodiak Island suggest a much lower value than that obtained for the Pribilof Islands. This estimate is complicated, however, by the overlapping foraging zones of different colonies and the greater incidence of transients,

such as shearwaters. These and other problems that beset attempts to generate valid estimates of seabird trophic demands are addressed.

## RELATIONSHIPS BETWEEN SCOTTISH SEABIRDS AND FISH STOCKS

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Applying a bioenergetics model to seabird communities in north Britain indicates that seabirds annually consume the energy equivalent of 20-30% of the annual production of zooplankton-consuming fish within a 50 km radius of their colony. This implies that seabirds, predatory demersal fish and industrial fisheries are in direct competition, such that an increased energy flow to one would be at the expense of another. Problems and uncertainties in the modelling will be discussed. The links between recent increases in Scottish seabird populations and changes in fish stocks resulting from overfishing will be explored and the possible influences of current trends in the patterns of North Sea fisheries on seabird populations will be outlined.

## DYNAMICS OF PAST AND PRESENT SEABIRD COMMUNITIES AND FOOD RESOURCES IN THE BENGUELA CURRENT REGION

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The fossil record and information on abiotic changes (e.g. sea level, temperature) in the Benguela Current region off the southwestern Cape, South Africa, from the late Miocene/early Pliocene to the present day is used to discover and explain changes in seabird communities and their food resources that have occurred over a period of seven million years. The breeding seabird fauna of the late Miocene/early Pliocene included penguins (Sphenisciformes) and petrels (Procellariiformes). These penguins are allied to modern cold water species and are suggestive of a colder climate at that time. Petrels no longer breed in the region. The present assemblage of breeding seabirds has existed since at least 100 000 years B.P. during the Pleistocene, although the relative proportions of species have altered. There were apparently more Jackass Penguins than Cape Cormorants during the last Glacial. Since the Holocene Cape Cormorants have been more numerous than penguins. The Cape Cormorant is now even more relatively abundant, probably due to a reduction in available prey size by commercial overfishing affecting penguins. However, no species has become extinct in the Benguela Current region in modern times; man's activities have "only" reduced numbers and affected relative proportions.

## IMPACT OF SEABIRDS ON MARINE RESOURCES, ESPECIALLY KRILL, OF SOUTH GEORGIA WATERS

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The food composition of the breeding population of South Geogia seabirds

during their breeding season is estimated using data, from studies conducted there, on breeding population size, timing and duration of breeding activities, energy costs of incubation in petrels, energy costs of incubation, moult and swimming in penguins and detailed information on the composition of the diet of all the eighteen main breeding species.

Existence and flight costs are estimated using standard equations and relationships. Chick energy budgets are calculated using data on meal size and the frequency with which chicks are fed. Costs of accumulating and restoring fat reserves are     assessed for the albatrosses and penguins, from information on weight changes throughout the breeding season. Demographic and ecological information are combined to estimate the consumption by failed and non-breeding birds.

Krill forms about 88% of the 2.7 million tonnes of food consumed, 80% of which is taken by camaroni penguins. Seasonal variation in krill consumption is analysed in relation to changes in the chemical composition of krill and preliminary information is presented on geographical variations in the impact of the seabirds on krill around South Georgia in relation to what is known of its distribution from acoustic surveys.

TROPHIC RELATIONSHIPS OF HAWAIIAN SEABIRDS AND
THEIR IMPACT OF MARINE RESOURCES

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Ten million seabirds of 18 species breed in the sub-tropical Northwestern Hawaiian Islands. The seabirds in this community weigh  between 0.05 and 2.8 kg and utilize a variety of strategies to partition available food resources. In addition to size and anatomical differences, they breed in different seasons, feed in different locations, and forage at different times of the day. All feeding occurs near the ocean surface, often in association with predatory fish such as tunas. A wide variety of marine organisms are eaten, but the most important are commastrephid squid and fish (often juvenile) in the families Exocoetidae, Carangidae, Mullidae, Synodontidae, Clupeidae, and Myctophidae. Most seabirds vary their diets by season and location, implying that they are opportunists and can exploit most any prey of suitable size in surface waters. This community therefore possesses a measure of resilience since many species can switch from one food source to another during times of food stress. On Laysan Island, an estimated 350.000 kg/day of marine resources are consumed by birds. The refinement of such an estimate of the daily impact of colonial seabirds on surrounding waters is contingent upon improved estimates of both daily food consumption and populations of seabirds. Complete assessment of the impacts of seabirds on local marine resources additionally requires a detailed knowledge of feeding areas.

BIOPHYSICS OF BIRD FLIGHT

Convener: W.Nachtigall (FRG), co-convener H.Oehme (GDR)


SURVEY OF THE BIRD FLIGHT RESEARCH IN THE USSR

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After a short review of attempts to elucidate the physical principles of bird flight in Russia a more detailed account was given of studies of bird flight mechanics by N.E.Joukowsky, one of the founders of modern aerodynamics almost 100 years ago. Problems of energetics in animal flight were already of interest for aerodynamicists and engineers in the early stages of aeronautics. Statics and dynamics of the locomotor apparatus were investigated. Substantial contributions to the investigation of bird flight were created by Soviet ornithologists during the last five decades in the field of comparative morphology and ecology. Prominent representatives of these branches were N.A.Gladkov and B.K.Stegmann. Extensive investigations of the bird's flying equipment and its evolution, alterations of proportions with respect to the function of the flying apparatus, connections of these interdependences with habits and environment brought up a lot of highly valuable results. In the last twenty years the analysis of mathematical and physical problems of bird flight grew more and more important. The publications of K.A.Judin, G.S.Shestakova and N.V.Kokshaysky are documents of the advances attained in this field by means of efficient methods of recording and experimenting. Finally very important contributions to the physiology of bird flight, especially to its energetics, emerged from investigations on bird migration, represented by prominent biologists as V.R.Dolnik and T.I.Blyumental. An enlarged version of this paper with appropriate bibliography entitled " Vklad otechestvennoy nauki v izuchenie poleta ptits" is published in Zoologichesky Journal 61, 971-987 (1982)


AERODYNAMIC ASPECTS OF FORMATION FLIGHT IN BIRDS

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In formation flight each bird flies in an upwash field generated by all other members of the formation. This leads to a remarkable reduction in flight power demand. Flight power reduction was calculated for arbitrarily shaped homogeneous and inhomogeneous formations in which birds of the same kind or birds of different span, planform shape and weight may be present. In the applied methods the beating wings of the birds were replaced by fixed ones. The calculations brought up that the total flight power reduction of the whole formation strongly depends on the lateral distance of the wings. A longitudinal displacement in flight direction has no influence on the total power reduction but only on their distribution on the involved individuals. Numerical examples were given which show the distribution of power reduction

in symmetrical and unsymmetrical V-formations. The local reduction is highest in the inner parts of the formation and decreases towards the apex and the side edges. Shapes of formation with almost uniform distribution of power reduction were found. In inhomogensous formations  wings, having larger span, lower aspect ratio or higher weight than the other wings act in such a way that the power reduction of the adjacent wings is increased. This influence is mainly percsived at the wing which immediately follows the varisd wing. The considerable benefit of saving energy by aerodynamic interference effects is thought to be the most important reason for the occurrence of formation flight. Beyond that also communication aspocts are present in formation flight. Under certain conditions formations are observed which are optimum-shaped from an aerodynamic point of view. In other cases non-optimal formations occur, in which an aerodynemic benefit is present in fact, but in which reductions of the possible power saving are accepted in favour of good optical contact. In the discussion doubts were uttered that the replacing of the beating wings by rigid aerofoils would perhaps create larger deviations. These objections were shown to be not valid in the case of restriction of the method to large and slow-beating birds where the influence of non-stsady events is very poor. The general conclusions were shown to be supported by observations of free flying gulls, geese and cranes.

ASPECTS OF HOVERING FLIGHT
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The prerequsite for calculating the mechanical power output is a knowledge as detailed as possible of the kinematics of wing motion. The possibilities of gaining these details were demonstrated. The principle is to construct an average bird of the species in question with characteristics of the geometry, the wing positions throughout the efficacious part of the beating cycle, the angular velocity during the downstroke and the temporal lapse of phases of the cycle. The basic data must be found from suitable large sampless of high-speed film analyses and morphological investigations. The physical model used for calculation shows some characteristics. The action of the wing upon the air does not start from the rest in each downstroke. The wing meets a vertical downwards velocity created by a horizontal oriented vortex ring which is formated at the end of the foregoing downstroke. This downstream is less than the induced wind at the level of the vortex ring but does not equal zsro. The resultant airspeed of a wing element depends on this downstream velocity, ths angular velocity of the wing, the position of the wing slement on the wing length and ths inclination of the plane of rotation against the horizontal. Forces and moments of force are calculated by the lifting line theory for that position of ths wings when their leading edges lay on a straight line in top view which is taken as representative for the whole downstroke. A variable circulation profile over the wing length is introduced. The momentary aerodynamic power is determined by the moment of force and the angular velocity. Using the time fraction of the

lift creating part of the cycle the circulation profile and the downstream velocity are altered until equilibrium of forces is reached. Special methods are necessary to find out the probably true value of flight power from a sample of solutions with respect to the accessory downwards velocity and the local lift coefficients of the wing. The procedure of calculation depends on the understanding of steady aerodynamics and for reason of the simplifications used it tends to bring values rather too small than too large. The calculated power-mass-relations of the three species while hovering ranged from 22 W/kg (Redstart) to 35 W/kg (Sparrow). The total mechanical power required for hovering is certainly higher because of the necessity to overcome the wing inertia at the beginning of the downstroke. The problem of converting the calculated values into metabolic power input was discussed. Recent statements on power input of starlings tested by the $D_2O^{18}$-method in near hovering flight lead to much greater figures of mechanical power if an efficiency of 0,2, in the flight muscles is assumed.

FLIGHT ENERGETICS AND BIRD FLIGHT IN WIND TUNNELS
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Results of investigations on power input of pigeons during long-time flights with respiratory masks in an open circuit wind tunnel. As to methodical details it was shown that the flight had to last much longer than 30 minutes, otherwise the birds would not reach a metabolic steady state. Handrised hybrids of English Tippler and Russian Griwuni pigeons proved to be the best experimental birds flying for 2 to 3 hours in continuous flapping flight with mask and tube. The characteristic data were the mass loss, the oxygen consumption, the carbon dioxide production and the respiratory quotient and their change with time and flight speed. The highest values of mass loss were reached at the beginning of flight. They decreased to a more or less constant one which was significantly less than at start. The mass loss as a function of time is described by an exponential function of the form $y = a + b \, e^{-kt}$ with the time t and the special constants a, b and K. The hypothesis seems well founded that at the beginning of flight the fuel consists mainly of carbohydrates with smaller energy content and that then the bird goes over to burning fat during long distance flight conditions. Minimal mass losses were found in the speed range of 11 to 13 m/s. The time course of the $CO_2$-production and of the RQ was quite similar to that of mass loss and were described by functions of the same type. The oxygen consumption increased suddenly after start, reached a maximum and after 10 minutes of flight held a nearly constant value which is a little lower than at beginning of flight. After landing oxygen consumption decreased rapidly to the preflight level. Steady state conditions of oxygen consumption were reached ten times as fast as in the other measured parameters. The mass loss though varying considerably in each individual pigeon and between the individuals ranged for normal wind tunnel flights like those measured in free flying homing pigeons. A mean power input of the investigated pigeons with a mass of 320 g was about 30 W at a minimum power speed of 12 m/s. In the discus-

sion a sufficient conformity was shown with a mechanical power output of 18
to 20 W/kg calculated for this speed with kinematical and morphological data
of feral pigeons. It was stated that the validity of theoretical calculati-
ons should be tested if possible by results of physiological investigations.


S Y M P O S I U M
GULLS, TERNS AND SKUAS
Convener: J.C.Coulson (UK)


DIETS AND FEEDING ECOLOGY OF GREAT SKUAS
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Diets of Great Skuas vary between different breeding sites in the North
Atlantic, and rates of population change can be linked to food availability.
Breeders, non-breeders and chicks differ in diet; reasons for the differen-
ces will be discussed. Food preferences can be inferred from correlations
between dietary composition and the effort expended by adults in obtaining
food. Coupling an assessment of the energy requirement of a Great Skua po-
pulation derived from bioenergetics modelling with the known dietary compo-
sition, the quantities of each food type consumed can be estimatsd. Compar-
ing this with the amount available provides an indication of the extent of
interspecific competition for food at whitefish trawlers which indicates
that this source of food may be of vital importance to the colonies of Great
Skuas in north Britain. The impact of kleptoparasitism and predation of
seabirds by Great Skuas will be outlined.

THE FEEDING ECOLOGY AND ANNUAL ENERGY DEMANDS OF
THE HERRING GULLS, LARUS ARGENTATUS
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Breeding, moulting and the depositing of winter or pre-migratory fat
reserves are events which are mutually exclusive in time in many bird spe-
cies, being essentially competing factors in the annual energy budget. In
Britain, the herring gull is commonly held to have a superabundance of food
throughout the year, in the form of domestic refuse. We have shown that
British breeding birds typically begin their annual primary feathsr moult
during incubation, and ths peak energy demands of moult coincide with the
feeding of large young. We have also examined seasonal changes in weight in
herring gulls throughout three full calendar years; all age classes gain
weight in winter (first year birds being heaviest), and begin to lose weight
in early spring. The adult birds reach their lowest weight at the time when
the energy demands of moult and breeding are high; peak adult mortality also
occurs at this time. These data will be examined with regard to the feeding
ecology and annual energy demands of breeding, moulting and winter-fattening
in the herring gull, and the extent to which refuse is a preferred or reser-
ve food source discussed.
1070

## FOOD CONDITIONS AND BREEDING SUCCESS OF TERNS

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Food conditions vary highly for tern populations annually and geographically. It is estimated in Finland that the food intake of an arctic tern chick is approximately 750 g from hatching to fledging and that of the common tern about 798 g, respectively. Thus the parents of the arctic tern have to gather about 1500-2250 g of food and those of the common tern about 1600-2400 g to rear 2-3 chicks to fledging.

In general, fish is the main source of food; and invertebrates (insects and crustaceans) provide a substituting source. The proportion of the components varies according to respective feeding conditions. In general, the conditions are more variable in oceanic areas, where winds, waves and tide have greater effects on food availability than in lakes and archipelago habitats with more sheltered shore waters.

The feeding conditions are reflected in different aspects of tern breeding biology, e.g. in laying time, laying intervals of successive eggs, egg size, clutch size, growth of successive chicks, and chick survival. The items are examined in the present paper.


## A REAPPRAISAL OF THE USE OF REFUSE DUMPS
## AS FEEDING SITES FOR GULLS (LARUS)

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The role of refuse dumps in the ecology of gulls has received little detailed and critical attention. It has often been assumed that the same individuals feed at dumps each day and that such sites are an "easy" source of food.

Evidence is presented that these assumptions are not always correct. There is a considerable exchange of individuals in time at dumps and feeding success is extremely uncertain depending on a series of chance factors. On some days individuals are unsuccessful in obtaining food. Further, there is considerable competition at such sites resulting in atypical age and sex rations among the gulls feeding on domestic refuse.

# ABSTRACTS OF POSTER PRESENTATIONS

RAPTORS IN EAST GEORGIA (RECENT SURVEY)
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26 raptor species have been recorded in East Georgia over 28 000 sq. km since 1976. Out of 26 species 16 were found nesting in the area. The Osprey, the White-Tail Eagle, the Steppe Eagle, and possibly the Peregrine Falcon have become extinct.

The Short-Toed Eagle (3-5 pairs), the Bearded Vulture (5-10 pairs), the Golden Eagle (up to 10 pairs) and the Black Vulture (10-15 pairs) are on the verge of extinction.

The Griffon Vulture (up to 40 pairs), the Egyptian Vulture (up to 80 pairs),the Lesser Spotted Eagle (70 pairs), the Booted Eagle (75-100 pairs) and the Marsh Harrier (20-40 pairs) are substantially reduced in number and breeding range. Not very numerous are Goshawk (150 pairs) and Hobby (150-250 pairs). The figures for the Sparrowhawk (250-350 pairs) are relatively constant, the same is true of the Black Kite (600-900 pairs), the Buzzard (1000-1300 pairs), the Kestrel (about 800 pairs).

Decline in population and range are mainly due to shifting habitats, decreasingly poor food availability, mortality of poisoned baits, disturbances at nesting sites, shooting, etc.

Though factually all raptor species are legally-protected, a more vigorous control for exercising the law is essential.

Setting up a number of birds' reserves and feeding grounds for scavengers is expedient. Wide-scale propoganda for the protection of raptors is to be kept on.

POLYGAMY IN THE PIED FLYCATCHER - IS IT MALE DECEPTION?
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In central Sweden, most pied flycatcher males, after having acquired a female, leave their first mate temporarily to attract another female. Up to 15% of the males are successful. All males return to their first female and feed her young. Although bigamous males sometimes feed the young of the second female, many of her young starve. Differences in mate and territory quality appear far too slight to make it advantageous for females to choose already mated males instead of unmated males. Females probably are not aware of the presence of other females of a male, and thus may pair up with bigamous males against their direct benefit. Males seem to hide their breeding status, as the two territories of a bigamous male are usually separated by several territories of other males.

1072

The benefit of becoming polygamous may be counteracted by an increased risk for polyterritorial males of being cuckolded. We found that tarsus length of nestlings was more closely correlated with that of the female than with that of the male at the nest. About 28% of the young are gathered by cuckolders in pied and collared flycatchers. In most cases the cuckolder is the male breeding in the nearest next box.

## CHANGES IN REPRODUCTIVE BEHAVIOUR OF BIRDS UNDER ANTHROPOGENIC INFLUENCES (EFFECTS)

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Birds' adaptation to antropogenic factors is often displayed in the changes of their reproductive behaviour. Unusual behaviour of black grouses and capercaillies is noticed at their mating places in the South Urals, in the traditional game-shooting regions. Groups of black grouses change their mating places daily moving on territories of thousands of hectares thus evading shooting from the ambush.

The capercaillie involved in reproduction fly from one place to another every 5-10 minutes without apparent cause, and many of their songs lack the "stone-deaf" phase.

18 cases of blackcaps nesting on the tree at the height of 2-3,5 metres were observed on the cattle pastures in the Volga region. Low-set nests are widely destroyed by the cattle.

In the city the incubation period of the magpie is being prolonged to 6-7 days, (n = 30) nestings of the lesser whitethroat stay in nest 15 days (n = 15), lesser whitethroat (n = 23) barred warbler (n = 9) and crested lark (n = 27). Nests are located higher: not lower than 7-8 m in the spotted flycatcher (n = 100), about 6-13 m in greenfinch (n = 200), more than 10 m in the fieldfare (n = 36). Urban white wagtails and wheatears nest above the earth in technical structures and buildings.

In Magnitogorsk and Sverdlovsk rooks nest on the transmission lines' supports (n = 34).

In Sverdlovsk in the nest of the Blyth's reed-warbler and the marsh warbler (n = 11). Sylvia borin (n = 5), the Great Rose Finch (n = 6) covering tray fully consists of snatches of thin copper wire. A lot of other behaviour changes in reproduction have also been recorded.

## EFFECT OF SPRING WATERFLOODS ON NESTING BIRDS IN THE VALLEY OF THE MID-OB RIVER

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Peculiar features of space distribution, periods and results of nesting for the basic bird species in the Mid-ob valley were studied for two different years: the year of 1978-79 with high spring water floods and the year of 1980 - with low spring waterfloods. Observation was made along the established study routes (15 km long) and over the testing grounds (24.6 ha), by the method of individual bird's markings.

It was found that high and prolonged floods resulted in shrinking territory for small Passeriformes nests (by 1.7-1.9 times), shorter distances between nests within the birds' colony (by 18-34%), greater density of nests (by 35-45%), lower reproduction rate (from 46.2% to 38.8% for Motacilla flava and from 51.1% to 42.8% for Emberiza aureola), the growing number of "reservist" non-breeding individuals. The following year due to the increased dispersal value of the young some changes in the sex and age composition in some resident Passeriformes were observed.

Low spring floods and the ensuing low summer level resulted in lower density, smaller bird productivity for the nesting Sandpipers (by 1.2-2 times), partial dislocation or disappearance of the Tern and Seagull colonies, decline in the number of breeders.

## ARBEITSREGIMES DES SCHALLSTRAHLENDEN SYSTEMS DES MITTELOHRES DER VÖGEL

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Ein einheitlicher Mechanismus der Arbeit des schallstrahlenden Systems mit zwei aneinandergebundenen Regimee ist ermittelt. Die Durchführung des Schallsignals im ersten Regime wird ohne funktionelle Teilnahme des Mittelohrmuskels verwirklicht. Der physische Faktor der Bewegung des Trommelfells und des Stapes ist die Energie der Schallwelle. Im ersten Regime vollzieht sich die Verstärkung oder die Abschwächung des Schalls nur dank der strukturellen Anpassung des äusseren und mittleren Ohres an die akustischen Bedingungen der Umwelt. Die Arbeit des Mittelohres im zweiten Regime ist mit der Funktion des Mittelohrmuscckels verbunden. Die Adaptationen des Gehörsystems, die die Empfindlichkeit des Gehörs bei den echolotenden Arten und den Arten mit entwickelter akustischer Kommunikation und Signalisierung erhöhen, charakterisieren sich durch das Vorherrschen des zweiten Regimes. Die regulierenden und Schutzprozesse in der Mechanik der Schallstrahlung werden in diesem Fall durch reflektore Zusammenziehungen des Mittelohrmuskels gewährleistet. Die Zusammenziehungen des Muskels werden vom zentralen Anteil des Gehörsystems nach dem Prinzip der Rückkopplung kontrollliert.

## FIRST PHOLOGRAPHS OF MEMBERS OF THE MESITORNITHIFORMES (MADAGASCAR)

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The order Mesitornithiformes consisting of three species in two genera is found only in Madagascar. The author was able to observe all members of the order in life. For the first time photographs were taken of living Monias benschi Oust Grandid and of living Mesitornis variegatus (Geoffr.), representatives of the two genera of the order.

Apparently no artist drawing illustrations of the Mesitornithiformes had seen living birds of this order so their representations, especially the body shape and posture, are unsatisfactory.

All Mesitornithiformes are inhabitants of the primeval forests where they search for their food among the leaf litter on the ground. Monias is found in the southwestern part of the island, Mesitornis variegatus in the northwest and Mesitornis unicolor in the east.

At least some of the species are supposed to be flightless, but the author was able to observe that all species can fly, even when they do so rarely. The systematic position of the group is still uncertain. In any case, they should not be placed in the Ralliformes (as is sometimes done), but they possess the status of a independent order, next to the Ralliformes, Eurypygiformes, Heliornithiformes, Gruiformes and others.

BRUTNACHWEISE DER ANATIDAE UND CHARADRIIFORMES AUF INSELN
TENDROWSKY MEERBUSEN SCHWARZMEER NATURSCHUTZGEBIET

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Charadriiformes sind die zahlreichsten und verschiedenartigsten Brutarten auf Inseln Naturschutzgebiet. Hier brüten 8 Arten Möwen und Seeschwalben: Silbermöwe, Schwarzkopfmöwe, Dünnschnabel-Möwe, Lachseeschwalbe, Raubseeschwalbe, Flußseeschwalbe, Zwergseeschwalbe. Die Anzahl der Schwartzkopfmöwe-population ist die höchste. Seit 1935 nahm die Anzahl der Brutpaaren mehr als um 12 Mal zu. Im Jahre 1981 beobachteten wir 275 530 Paaren.

Die zahlreichste Art unter Seeschwalben ist die Brandseeschwalbe. Aber ihr Bestand schwankt von Jahr zu Jahr, die höchste Zahl (30 806 Paaren) bobachteten wir 1981. In den 70 Jahren ist die Raubseeschwalbe zur gewöhnliche Brutart geworden. Früher brütete diese Art sporadisch. Hier finden wir 4 Brutarten Haematopodidae: Austernfischer, Seeregenpfeifer, Rotschenkel, Säbelschnäbler. Im letzten Jahrzehnt vermehrte sich die Anzahl der Inselpopulation dank der Übersiedlung aus der salzhaltigen Steppe.

Anatidae: sind die zahlreichen Brutarten, Brandgans, Stockente, Schnatterente, Mittelsäger. In den letzten 25 Jahren vergrößerte sich die Anzahl dieser Arten um 9 bzw. 24 Mal. Bedeutend weniger brüten Spiessente, Löffelente und Knäkente. Eine neue Brutart-(Kolbenente)-erschien. Die Brandgans baut ihre Nester auf den Inseln nicht in Höhlen.wie gewöhnlich, sondern auf der Oberflache auf verschieden Pflanzen.

THE INFLUENCE OF FEEDING THRESHOLD LEVELS OF p,p'-DDE
ON PHYSICAL AND PHYSIOLOGICAL PROPERTIES OF EGGS OF THE
RINGED TURTLE DOVE (STREPTOPELIA RISORIA)

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Ringed turtle dove (Streptopelia risoria) eggs and reproduction are known to be affected by pesticides. We tested the influence of threshold doses of p,p'-DDE (DF, $0.1-6.3$ mg·kg$^{-1}$BW·day$^{-1}$) on DDE concentrations in eggs (DE, mg·kg$^{-1}$), egg mass (W), egg surface area (A), shell mass (Wsh), eggshell thickness (L), yield point (breaking strength, F), eggshell water vapour diffusive conductance ($G_{H_2O}$), prepipping $O_2$ and $CO_2$ aircell gas tensions ($P_{AO_2}$, $P_{ACO_2}$), and female productivity. 20 pairs were maintained in individual 27x35x54 cm cages, at $25\pm2°C$, 16 hours light and 8 hours darkness, and

fed enriched sorghum ad lib. Females were daily administered DDE orally in
1 ml soybean oil for 60 days. Eggs were collected to initiate a new egg
laying cycle and some were artificially incubated at 38°C $\pm$0.5 and 51% RH
$\pm$3. DE as a function of DF was: DE = 0.89+0.23 log DF $\pm$0.26 SEE ($r^2$ = 0.919).
W, A and Wsh dropped significantly (p $<$ 0.01) at DF = 0.6 mg·kg$^{-1}$ by 7%
$\pm$2 SD, 3% $\pm$1 SD, and 4% $\pm$1 SD, respectively. No significant change in L
could be detected up to DF = 3.0 mg·kg$^{-1}$BW·day$^{-1}$. Yield point dropped con-
tinuously from an average control value of F = 218 g $\pm$7 SD at a rate of 19 g
per mg DF, to a plateau at 79% $\pm$5 SD. $G_{H_2O}$, $P_{AO_2}$ and $P_{ACO_2}$ were normal and
not affected by DF in the range tested. Clutch size dropped from 1.9 to
1.2 eggs at DF = 6.3 mg·kg$^{-1}$BW·day$^{-1}$ and total productivity dropped from
4.3 to 1.5 eggs per month. It is concluded that the amounts of DDE transfer-
red to eggs increase relatively little with augmented parental contamination
levels. Practical indicators for low DDE levels in this species are egg mass
and yield point reduction.

BONY-TOOTHED BIRDS·(ODONTOPTERYGIFORMES HOWARD, 1975).
SYSTEMATICS. DISTRIBUTION. CASPIODONTORNIS KOBYSTANICUS SP.
FIRST BONY-TOOTHED BIRD FROM USSR

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Bony-toothed Birds (Odontopterygiformes) are a separate order which have
four families (Harrison and Walker, 1976). But Bony-toother  Birds are one
suborder of the Pelecaniformes according to other taxonomists. Most ancient
records of the Bony-toothed Birds date by Lower Eocene (Odontopteryx and
Pseudodontornis longidentata from London Clay). The records of the Bony-
toothed Birds were restricted to England, France and to North America before
1977. Position of Gigantornis eaglesomei from the Nigerian Middle Eocene
between Bony-toothed birds are doubtful. The sternum of this genus is found,
but cranial structures are unknown. The cranium and the mandible of Bony-
toothed Bird were in the sea deposits of the Middle Oligocene near the Pe-
rikishkul Village (East Azerbaijan) in 1977. This bird was described as Cas-
pidontornis kobystanicus by Aslanova and Burchak, 1982 (Pseudodonornithidae).
Caspidontornis was the water bird the size of the pelican. The Caspidontor-
nis's teeth of the mandible and maxilla are situated vertically in front of
the beak, but behind it are inclined on. The teeth alternation are large,
small, middle, small, large, etc.

STRUCTURE OF BILL TIP ORGAN IN ANSERIFORM BIRDS

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Structure of mechano-receptor complexes forming cara papillas in the
lower jaw and corn cups in the upper jaw are dealt with herein. Data on 27
Anseriform species of the USSR fauna are discussed and a number of tribes
such as Anserini, Tadornini, Anatini, Somaterini, Aythini, Mergini are
compared.

The lower jaw apparatus is found to be more developed in dubbling ducks and other strainers who are food-searching in water or mud, often at night. The upper jaw apparatus is found to be more developed in grass-eating species searching for ground food. Receptor complexes in mollusk-eating species are big and rough while in invertebrate-eating species they are thin and long. Sometimes these complexes within the same species diverge in size and shape. Birds feeding on water vegetation, such as the mute swan, possess the peculiarities of both the dubbling duck and those of the grass-eating species.

EFFICIENCY OF FOOD UTILIZATION DURING MIGRATORY
FATTENING IN THE GARDEN WARBLER (SYLVIA BORIN)

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The efficiency of food utilization during migratory fattening in the Garden Warbler was examined under constant conditions. The main goal of the experiment was to test whether body weight increase in a passerine bird during migratory fat disposition is only due to hyperphagia or whether other mechanisms such as changes in the efficiency of food utilization are involved. It was found that the efficiency of food utilization defined by "daily body weight gain (g)/daily food intake (g)" increases during migratory fattening. The results are discussed in relation to the underlaying mechanisms and in relation to an optimal feeding strategy of a migratory bird.

HOMING PERFORMANCES IN THE SAND MARTIN (RIPARIA RIPARIA)

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The homing performances of Sand Martins (Hirundo riparia) breeding in three colonies located along two tributaries of the Po River (Northern Italy) have been tested with the classical method of registering both the vanishing points at the release site and the recoveries at the colony. Sand Martins were caught at the colony by mistnets and by "funnel traps" placed directly at the entrance of the nest hole. Within three hours of the capture the birds were released at two opposite sites, NW and SE with respect to the colony, at distances of 28 and 67 kms respectively.

A total of 102 individuals have been singly released and 81 vanishing points was obtained. In the release tests performed we found a nonrandom distribution of vanishing points in five cases out of six (Rayleigh test) and an homeward orientation in four out of six (V test). Furthermore at 20 and 40 seconds after release, some birds were already homeward oriented (3 and 4 out of 6 respectively).

The return rate was measured in two tests, with results of 40.7% from the nearest release-site and of 44% from the farthest one.

Biometrical data were also taken to characterize the population studied.

PHYLOGENY OF THE RATITES AND COMMENTS ON THEIR ORIGIN
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A study of the gross structure and ultrastructure of ratite feathers,
based on biometrical and morphological data confirms some of the postulated
relationships among the ratites. Supporting evidence is provided by the
osteology, structure of the egg shell and other features of fossil and liv-
ing ratites. Some trends can be shown in ratite feather structure. Our study
permits further comments on the origin of this group.

DISTRIBUTION AND POPULATION OF HERONRIES IN ITALY
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In the first national census of Italian heronries (1981) we checked 57
colonies, out of a total number of about 60, plus some small groups of Purp-
le Herons. Most heronries were in Northern Italy, 2 in Central Italy, 1 in
Southern Italy, 1 in Sardinia, 30 colonies were concentrated in the small,
North-Western zone of intensive rice cultivation, 6 were along the Po River,
and 10 on the coastal lagoons of the northern Adriatic Sea.

Counts of the nests were difficult to make because many heronries were
large, inaccessible, and mixed species, but in 35 colonies nests counts were
correct within a 5% range of error. The total number of censused nests was
(most likely estimate and probable range):

| | | | | |
|---|---|---|---|---|
| Night Heron | N.nycticorax | 17.300 | (15800 / | 20.200) |
| Little Egret | Egretta garzetta | 6.600 | ( 5600 / | 8.300) |
| Grey Heron | Ardea cinerea | 690 | ( 640 / | 740) |
| Purple Heron | Ardea purpurea | 450 | ( 350 / | 660) |
| Squacco Heron | Ardeola ralloides | 150 | ( 100 / | 200) |

In the main range in the Po plain  the Grey Heron breeds only in the west
and the Purple in the east; the other species are widely distributed, but
the Night Heron is more abundant in the rice fields zone and the Egret in
the coastal lagoons. These differences in distribution may be related to the
preferences in feeding habitats of each species.

The very high density of Night Herons (about 1.5 times the censused po-
pulation for all the rest of Europe) may be explained by the presence of
large areas of rice fields, used by these birds as feeding zones.

STRUCTURE OF MIXED-SPECIES FLOCKS OF TITS
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Tits and related bird species were examined at Pechoras, the Pskov region
in 1968-1969. Various species were observed in the mixed-species flocks
(n=762) with the following frequency: Parus montanus - 74.9%, P.cristatus -
68.3%; Regulus regulus - 56.5%; P. major - 33.7%, Certhia familiaris - 19.3%;
Sitta europaea - 17.1%; P. ater - 13.9%; P.palustris - 12.6%; Aegithalos
caudatus - 8.0%; P.caeruleus - 3.9%. Floks made up basically of P. montanus

and P.cristatus were most common. Their main features are: 1) adult pairs are established and keep within the same territory of  10 ha; 2) the young after postfledging dispersal become resident and settle on the adults' territory. The newly-formed social groupings are established all through autumn and summer; 3) the territories of groups P. montanus, P.cristatus, P.palustris coincide. The territories of S. europeaa pairs include 2-4 territories of Tits communities; 4) P. montanus, P. cristatus, P. palustris, P. ater, S. europeae store large amounts of food, which is later used collectively. The non-storing birds sponge on the other species; 5) because of the adult bird's attachment to particular dwelling sites, mixed-species flocks of Tits tend to occupy the same territory year after year.

Mixed-species flocks formed of A. caudatus or P. major groups have a different structure.


MORPHO-ÖKOLOGISCHE ADAPTATIONEN VON ZENTRALEN ABSCHNITTEN
DES HÖRSYSTEMS DER VÖGEL

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Die morpho-ökologische Analyse des zytoarchitektonischen und Neuronenbaues der akustischen Zentren der Medulla oblongata und des Mittelhirns ist bei den Vertretern von 6 Ordnungen (14 Arten) Bodenvögel mit verschiedener Stufe der Spezialisierung des Hörsystems und bei den Vertretern von 4 Ordnungen (10 Arten) Wasservögel durchgeführt worden.

Bei den Bodenvögeln, deren Gehör verschiedene Rolle bei der Nahrungssuche und in der akustischen Kommunikation spielt, kennzeichnet sich die Veränderlichkeit der zytoarchitektonischen Charakteristiken durch die Veriationen der Anzahl von Neuronen mit langen Axonen und durch die räumlich-funktionelle Verbreitung. Die Veränderlichkeit der Neuronenformen kennzeichnet sich durch den Ausmass, Verästelung und Fläche der Dendriten, wodurch die Veränderung des afferenten Feldes von Neuronen bestimmt wird. Die Angaben über die Neuronenzahl in Hörkernen der Medulla oblongata und des Mittelhirns aller untersuchten Vogelarten sind angefüht, sowohl die Schemen der Neuronenstruktur von kochlearen Kernen, des laminaren und vorderen olivaren Kernes der Medulla oblongata und dorsalen mesenzephalischen Kernes.

Bei den Vertretern von Wasservögeln sind keine bedeutende Schwankungen von Zahlcharakteristiken der akustischen Zentren nachgewiesen. Die Neuronenformen dieser Arten sind bedeutend einförmiger und einfacher, als diese bei den Bodenvögeln. Die Gruppe der Pinguinen zeichnet sich aus: hier ist bei zwei Gattungen die Reduktion des Abschnittes des akustischen Zentrums der Medulla oblongata festgestellt. Auf diesem Niveau verwirklicht dieser Abschnitt die Verbindung des Hörsystems mit den motorischen Zentren.

PRIMARY SUCCESSION OF BREEDING BIRDS COMMUNITIES
IN DUNES ON THE SOUTH COAST OF THE BALTIC SEA
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Studies were carried out in the central part of the Polish Baltic coast
in 1971-77. Censuses were made during the inbreeding seasons, using mapping
technique, in nine plots of 14.5-75 ha (total area 262 ha) covering the full
succession of coastal vegetation: sandy beach, white dunes, open dark dunes,
dunes with single trees and small clumps of trees and bushes, dunes with
numerous single trees and greater clumps of young pine forest, young and
older pine forests, 130-years-old coastal pine forest.

It was shown that the number of bird species increases steadily from 3
to 25 depending on the stage of the development and complexity of the vege-
tation. The density of pairs attains the maximum in the pine-forest 31-45-
years-old (29.6 pairs per ha) and then decreases in older forests. In the
studied successional series, one can distinguish three main types of bird
communities which are characteristic for beaches, dunes and coastal pine-
forests. The transition of a community into the next one is accompanied by
almost complete changes in species composition, their diversity and struc-
ture of dominance. It is caused mainly by high dominance of only one or two
species. For example, Alauda arvensis dominates in open dunes (85% of all
birds) but Fringilla coelebs and Phylloscopus trochilus in initial stages
of a forest (together 67%). There are also changes in the proportions of
birds representing different modes of nesting, feeding and singing. For
example birds singing and displaying in the air dominate in early stages
whereas singing on perches dominates in mature forest.

SUCCESSION OF BIRD COMMUNITIES ON SPOIL BANKS
AFTER SURFACE BROWN COAL MINING
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This study examines the course of primary succession of bird communitiss
on spoil banks after surface brown coal mining in northwestern Bohemia (Cze-
choslovakia). Bird population changes were studied on spoil banks from initial
stage 2-3 years after heaping ($N_1$) to 6 and 25 years ($N_2$, $N_3$) after heaping
and 6 and 20 years ($R_1$, $R_2$) after reforestation to a mature oak wood (M) out-
side the spoil banks.

All qualitative and quantitative characteristics increased from $N_1$ to M
stage with exception of a decrease in first years after reforestation ($R_1$).
Species numbers and total densities were as follows: $N_1$ - 3 species and 1.8
pairs per 0.1 $km^2$; $N_2$ - 6 and 18.3; $N_3$ - 12 and 24.8; $R_1$ - 6 and 16.0; R -
14 and 41.0; M - 23 species and 79.2 pairs per 0.1 $km^2$. Indexes of species
diversity (H'): $N_1$ - 1.56; $N_2$ - 2.49; $N_3$ - 3.21; $R_1$ - 2.13; $R_2$ - 3.58; M -
4.06.

In initial stages, distribution of relative species frequencies reached
the distribution of the geometrical series (especially $N_1$, $N_2$) and gradually

changed ($N_3$, $R_1$) into the distribution comparable with the k-variant of the Dirichlet distribution ($R_2$, M), which is typical for well-developed bird communities.

The bird community in young forest stage ($R_2$) showed in this study a high similarity with the community in mature oak forest (M).

## SPATIAL AND TEMPORAL DISTRIBUTION OF TERRITORIAL ACTIVITY IN SONGBIRDS

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The spatial and temporal distribution of full songs and other activities were studied for whole days during the breeding period in individual free-living Chaffinches (Fringilla coelebs) and Willow Warblers (Phylloscopus trochilus). From these data, quantitative territory maps and actograms were derived. While song and agonistic activity (per definition) as well as sexual displays were confined to the territory in the Chaffinch, some feeding and comfort behaviour took place outside ("home range"). Singing activity was strongest in the early morning, but continued throughout midday and, after a decline in the afternoon, reached a brief and small maximum in the evening. No clear bimodal distribution was found. The bulk of the songs concentrated in the center not at the boundaries of the territory while the area immediately surrounding the nest site was avoided to a certain degree. This type of spatial distribution was most marked in the early morning, and decreased in the course of the day or shifted considerably to agonistic interactions with conspecific neighbours. The percentage of incomplete songs or different song types did not differ with regard to the site of song posts or day time.

## POPULATION CURVES OF SOME SMALL HOLE-BREEDERS IN CENTRAL EUROPE FROM 1927 TO 1981

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The presented population curves of Blue Tit (Parus caeruleus), Nuthatch (Sitta europaea), Redstart (Phoenicurus phoenicurus) and Wryneck (Jynx torquilla) are based on numbers of breeding pairs in nestboxes. The data were compiled from Central European study areas by the authors and other informants for the last 55 years. In the Braunschweig district (from 1954-1981) the results are based on checks of an annual average of 400 nestboxes.

In spite of frequent and sizeable fluctuations in the populations of the Blue Tit (max. 120, min. 31 pairs/1000 nestboxes) and the Nuthatch (max. 30, min. 12 pairs/1000 nestboxes), both species show neither a long term increasing nor decreasing trend. The striking fluctuations from one year to another are more easily explicable in terms of the species-specific behavioural repertoire (e.g. irregular migratory movements, considerable susceptibility in winter) than by the relatively slight differences in annual reproductive efficiency.

Redstart (at least from 1955-1981) and Wryneck (since 1927) populations showed a significant decrease. In the period under investigation no changes in the reproductive efficiency, measurable as a trend, could be discerned. The authors believe it possible that influences during migration and/or in the winter quarters are responsible for the declines.

## AKUSTISCHE SIGNALISIERUNG STRUTHIONIFORMES, RHEIFORMES UND CASURIIFORMES IN FRÜHER ONTOGENESE

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Im Naturschutzgsbiet "Askania-Nowa" wurde die Entwicklung der akustischen Signalisierung Struthio camelus, Rhea americana, Dromiceus novae-hollandiae untersucht. Nach funktionellen Merkmalen und struktureller Anordnung sind die ermittelten Laute den Lauten anderer nestflüchtender Vögel in der Periode der frühen Ontogenese ähnlich. Die Analyse der akustischen Signale und der Morphologie des unteren Kehlkopfes srmöglicht das Vorhandensein gemeinsamer "primitiver" Mechanisme der Schallstrahlung in pranatalsr und früher postnataler Ontogenese der Vögel snzunehmen. Diese Art der Schallstrahlung charakterisiert sich durch die glockige Form der Frequenzmodulation und vsrwirklicht sich ohne Nervenkontrolle über Spannung membrana tympani. Die "primitive" Art der Schallstrahlung in frühen Stadien der Entwicklung der akustischen Signalisierung ist für Vögel im allgemeinen eigen. Eine stabile Spannung der inneren membrani tympani wird in dieser Periode wahrscheinlich mittels m. tracheolateralis errungen. Die Formänderung der Frequenzmodulation wird sowohl durch die Spannungänderung membrani tympani, als auch durch die Geschwindigkeit des Luftdurchflusses bestimmt.

## MIGRATIONS DE TRAQUET ISABELLE (OENANTHE ISABELLINA) EN L'URSS ET SON PROBABLE RÔLE DANS LE TRANSPORT DE L'AGENT DE LA PESTE

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Comme espècs de fond des déserts et steppss de l'Europe et de l'Asie, le TRAQUET ISABELLE est étroitement lié aux rongeurs dans lss naturels foyers de la peste. Ses migrations saisonnières et déplacements locaux contribuent à la diffusion des puces (plus ds 25 espèces) et des ixodss dans le terrain et donnent la possibilité de transport du microbe de la peste (Sergueev, 1936; Bibikov, Bibikova, 1956; Kalaboukhov, 1969, etc.). Les Traquets non seulement transportent mais aussi diffusent les ectoparasites sn vastes espaces de la région de leur nidification et leur hivernage. Les observations des voies et de la vitesse (en moyenne, 200-300 km en vingt-quatre heures) des migrations saisonnières de miliions d'individus de Traquet isabelle permettent de supposer la possibilité de transport du microbe de la peste par les oisaux malades à grandes distances. D'après l'expériment, on a constaté la perte d'un quart de population de Traquet isabells le 10-e - 19-e jours après la contagion (Peyçakhix et d'autres, 1969, 1970). Malgré l'absense d'étude systématique on connaît déjà des cas d'isolement de microbe ds la peste du Traquet

1082

isabelle et de ses parasites en Altaï, dans les régions entre les fleuves Volga-Oural et Oural-Kouchum, à Daghestan et en Mongolie (Chevtchenko et d'autres, 1980).

## ADAPTIVE STRATEGIES OF BIRD BEHAVIOUR IN A BIG CITY

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In the Moscow area (about 900 km$^2$) there nest 110 bird species, the city being a survival habitat for many of them. Urbophobous birds (i.e. the majority of birds) are retained where their natural habitats are preserved. The urban avian fauna is composed of urbophiles (synantropes including) and predominantly of species with labile behaviour (Corvidae, Sturnidae) since behaviour is the main pathway of adaptation to urban conditions, which are fairly complex and varied. In many cities the number of Corvidae increases rapidly, each city with a dominant species: the hooded crow in Moscow, the raven in Riga, the rook in Lublin, the magpie in West Berlin and Gorky, the jay in Kharkov, the jackdaw in Tartu, etc.

Selection has given rise to populations with a considerably weakened man-fright reaction. This is primary adaptation. Just like the tamest cage birds, as was observed by D.K.Belyaev, quiet and fearless urban crows develop changes in timing and periodicity of breeding. Drastically changed are the population demographic structure and nesting behaviour such as "balcony" starlings and tits, crow nests ostentatiously open in crowded places, their nest ranges being reduced by dozens of times. In food behaviour, stable individual habits are due to imitation. Thereby, the number of trained birds is ever increasing, involving, in certain cases, the entire population.

At a certain urbanization stage, migratory birds such as rooks, starlings, mallards (the three latter species from 1960ies-1970ies) settle down by retaining populations wintering in cities.

Differentiation of ecological features in urban and non-urban populations results in ecological isolation.

## AGE-RELATED ASPECTS OF DIVING BUCK REPRODUCTION

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An intensive long term banding program at the Engure Marsh, Latvia(north-west part of the USSR) has established a marked population of female Pochard and Tufted Duck of known age. Physical condition of females (body weight and wing length), clutch size and egg volume as well as duckling weight and survival varied with age of parent female. Yearlings nested later, and their clutch size, egg volume and one-day-old duckling weight were lower. The mean clutch size decreased as season progressed. This relationship held when single age classes were examined. Survival of offsprings produced by year-lings was significantly lower than that produced by older breeders (measured by random recovery rate and recruitment rate of females to the native marsh). Pochard females nesting in habitats of different quality exibited signifi-cant differences in their morphological and reproductive characters; female condition, egg volume and one-day-old duckling weight of the same age cohort

1083

were higher in the optimal nesting habitats. Pochard yearlings were found to nest predominantly in sub-optimal habitats. Age-related differencies of parent females play an important role in the self-regulatory process of population numbers (see Mihelson et al., this issue).

NESTING OF COMMON AND LITTLE TERNS (STERNA HIRUNDO AND
STERNA ALBIFRONS) ALONG THE PO RIVER
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The inland population of Common and Little Terns nesting along the Po, the chief river in Italy, was cansused in 1981. Over a 536 km stretch of the river, from Turin to the Adriatic Sea, we found 35 colonies, with a total population of 353 pairs of Common and 405 of Little Terns. In many of the colonies the Little Ringed Plover (Charadrius dubius) was also found to be nesting. There were more colonies in the higher reaches of the river than in the lower, where the river is partially canalized. The mean number of nests, with a maximum of 10 per km, was positively correlated in the various sections of the river, to the amount of low and/or stagnant water and with the number of islets.

The nesting population is stable, as may be seen from the partial counts made from 1977 to 1980.

Nests were placed mainly on sandy or pebbly islets without any vegetation or on open banks. Both species use little or no material to line the nest, which are very scattered, having a mean nearest neighbour distance of 10. $3\pm5.6$ m in the Common and $4.3\pm3.6$ m in the little Tern.

SECONDARY SUCCESSION OF BREEDING BIRD COMMUNITIES
IN DRY PINE-FORESTS IN POLAND
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This study was made in a large area of uniform pine forests on poor sandy soils in northern Poland in 1978-80. The field studies were done with two methods: the mapping technique (at least 5 repeated censuses on 14 plots; sampled area - 165 ha) and the "taxation method" (censusing once but on many dispersed plots representing 9 age-classes of forest; sampled area - 678 ha). The first one gives an accurate number of birds inhabiting particular plot but the second provides a list of potential inhabitants of particular type of vegetation. Results differ slightly but biocentic indices are comparable.

The crucial stages of succession of bird communities according to the age-classes of trees are: (1) the open clearing (up to 7 years), only birds of open country; (2) the brush (8-20), birds of coniferous bushes, increasing density of pairs, absolute dominance (more than 50%) of Phylloscopus trochilus; (3) the thicket (20-30), poor breeding avifauna, formation of a forest bird fauna, increasing species diversity, decreasing density; (4) the pole-tree stand (30-60), formation of the pine-forest avifauna, density and diversity relatively low and stable; (5) the young forest (60-80), rapid increase

in diversity and in density, absolute dominance of <u>Fringilla coelebs</u>; (6) the matured forest (80-100), increasing portion of holenesters, absolute dominance of <u>F.coelebs</u>, further increase in diversity but stability in density; (7) the old pine-forest (more than 100 years), greatest diversity and richness of bird community, stability in species diversity but further increase in density.

RECORDING OF BIRD VOICE AT THE BRITISH LIBRARY
OF WILDLIFE SOUNDS
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British Library of Wildlife Sounds,  The British Institute of
Recorded Sound, 29 Exhibition Road, London SW7 2AS, UK

The British Library of Wildlife Sounds contains about 8 000 separate tape recordings of some 2 000 animal species, the majority of them of birds. B.L.O.W.S. also holds copies of all the natural history recordings in the B.B.C.'s sound archive, comprising 6 000 recordings of about 1 500 species, well over half being of birds. It also houses over one thousand gramophone (phonograph) records and cassettes of wildlife sounds, published between 1910 and 1982, again mostly presenting avian sound production. Co-founded in 1969 by Patrick Sellar and Jeffery Boswall as a new department of the British Institute for Recorded Sound, B.L.O.W.S. was inaugurated by David Attenborough and its full-time curator is Ron Kettle. The recordings come from all the zoogeographical regions of the globe, but particular emphasis is placed on the western Palearctic and Antarctica.

The B.I.R.S. provides a free listening service. The opening hours are 10.30-1.00 and 2.30-5.30, Monday-Friday. It is advisable to make an appointment beforehand. Copies of most tape recordings and B.B.C. Sound Archives recordings in B.L.O.W.S. can be supplied for scientific study on payment of a service fee and the completion of an agreement limiting their future use, and protecting copyright. Offers of recordings are welcomed, and the Curator will be pleased to supply details of how to contribute. If original recordings are deposited, copies can be supplied to the contributor without charge. Depositors have the satisfaction of knowing that their work will be preserved for posterity and, provided they give agreement, made available for research. In all cases the recordist's copyright is protected, and there is no restriction on putting the recordings to any further use whatever. The B.I.R.S. will supply blank tape for use on approved projects, subject to a signed agreement that copies of all recordings will be deposited in B.L.O.W.S. under the usual terms. B.L.O.W.S. includes a collection of books and other printed material relating to bio-acoustics. Discographies and other articles about wildlife sound are published from time to time in the Institute's journal, "Recorded Sound", and further scholarly contributions are welcomed. Three special issues, nos. 34, 54 and 74-75, marking the opening, the fifth and tenth anniversaries of B.L.O.W.S. respectively, were devoted entirely to wildlife sound. Leaflets about B.L.O.W.S. are available at the site of the poster.

SOCIAL RELATIONSHIP AS A VARIABLE IN REACTIONS   TO ALERT,
ALARM, AND ASSEMBLY CALLS AMONG COMMON CROWS (<u>CORVUS</u>
<u>BRACHYRHYNCHOS</u>)

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The Common Crow (<u>Corvus brachyrhynchos</u>) of North America is a social
species in which groups of individuals often harass a predator. I have in-
vestigated the effect of the social relationship between sender and receiver
in determining responses to various calls given in contexts involving poten-
tial danger. Four types of calls were tape recorded from each of 6 individual
crows and played back to 7 captive Common Crows. The taped senders were eit-
her well-known (e.g., cagemates), somewhat familiar, or unfamiliar to the
receivers. Responses of each receiving bird were monitored by tape record-
ing, and direct observation in some cases. Results were analyzed to deter-
mine differences in response with respect to sender-receiver relationship;
responses to playbacks are also being compared with responses to naturally-
occurring vocalizations of different senders.

Results are discussed in relation to crow social organization.

THE INFLUENCE OF MOUNTAINOUS AREAS ON BIRD MIGRATION

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There is ample evidence that mountainous areas have an influence on bird
migration. However, detailed studies on the degree and nature of these in-
fluences on the general course of migration, on different bird species, po-
pulations and age-groups are largely lacking. It is the aim of a new nation-
al research program to concentrate bird migration research in Switzerland
on the study of migration in the area of influence of the Alps, in order to
develop models on migratory strategies related to mountainous areas.

This presentation aims at a stimulation of discussion on observed or sup-
posed influences of mountain ranges (and other barriers) in different parts
of the world.

.Mountainous areas may have (actually or through selection) different
meanings for migrating birds, such as: areas with limited food resources or
with improved food-resources (owing to later vegetation period or migrating
insects); unfamiliar habitat; limited range of visibility; turbulent, ir-
regular and unpredictable airflow; protection against unfavourable winds;
updrafts; retarded movements of weather systems, followed by sudden weather
changes; optical or physical barriers causing vertical or horizontal deviat-
ions in flight paths (and thus impeding orientation); lower temperatures and
decreased oxygen pressure at higher flight levels; leading-lines; releasers
of innate shifts in the primary direction; and other factors.

CLASSIFICATION OF BIRD POPULATIONS OF THE USSR

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The **subject** of classification and mapping is the territorial groupings of

summer and winter populations of birds of basic habitats. The populations are classified according to two parameters: the similarity in the ecology and storey structure, and the share of different geographical-genetic groups in bird populations. At the first stage of classification of populations according to the ecology and storey structure, groupings are singled out with predominance of birds most differing in ecology (with predominance of forest birds, birds of open habitats, water-bog birds, etc.). At the next two stages, the populations are classified according to participation in them of birds of different storey groups. At the first stage of classification according to the share of different geographical-genetic groups in bird populations, groupings are distinguished with predominance of birds of major independent geographical-genetic groups; at the second stage the populations are classified according to participation in them of birds of subgroups distinguished within these groups.

When preparing maps of summer and winter populations of birds of the USSR, the legend is planned to be of three parts, viz., matrix-legend, textual legend and supplementary designations. Classification of populations according to ecology and storey structure is given in vertical columns of the matrix-legend, and classification according to participation of different geographical-genetic groups and subgroups in bird populations - in horizontal columns. The textual legend shows the dominant and co-dominant species in the populations, and also which types of habitat these populations are characterized by. The total summer density of bird populations in one or another type of habitat is shown by hatching of different closenesses in the supplementary designations of the map of summer populations, and in those of the map of winter populations - by how many times the density varies from summer to winter.

STUDY OF SOME ASPECTS OF THE MOBBING-BEHAVIOUR OF THE
STARLING (STURNUS VULGARIS VULGARIS L.)

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Mobbing in the starling occurs during the reproduction period. Upon seeing a living little owl (Athene noctua (SCOP.)) a nestowner reacts with calls ('screaming alarm', 'spet' call), a wing- and tail-flick, 'Daanje'-flight around the owl and sometimes even pouncing on the predator. In a breeding colony, other starlings generally join the first one.

Our observations (1980-1981-1982) allow a detailed description of the reaction (kind, intensity, latency, course, after-discharge, habituation phenomena, the course of the mobbing-behaviour during the reproduction period). Mobbing by starlings shows important fluctuations during the year, with a peak during the breeding-season.

The releasing factors causing this behaviour include both external and internal components. We report on experiments carried out in 1982 both in captivity and in the field:

1. External factors. The mobbing reaction resulting from a) visual stimuli of a little owl (Athene noctua (SCOP.)), a squirrel (Sciurus vulgaris L.)

and a domestic cat (<u>Felis catus L.</u>), and b) acoustic stimuli of sounds uttered by the other starlings while mobbing. This will examine the possible communication function of these sounds.

2. Internal factors. The relations between the testosterone level in the starlings and its reaction to owls.

TROPHIC EFFECT OF BIRDS IN STEPPE FORESTS OF THE UKRAINE
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There are more than 230 species of birds of various phenological and trophic groups in steppe forests of the Ukraine. The annual consumption of the biomass by all birds in different types of forests totals 3.5-23.3 t/km$^2$, where phytomass constitute 32.5-41.3% and zoomass 58.7-67.5%. Consumed biomass by phytophages constitutes 41.2-47.6%, zoomass of entomophages - 10.2-13.0, that of predators - 0.004-0.05%. Birds affect about 400 invertebrate phytophageous species and 10 species of rodents.

In July the birds reduce phytophageous biomass by 4.8% in damp ash-oak forest, by 8.7% in dry pine forests and by 2.9% in ash-oak plantings in placor plain. In the forest biogeocenoses, the biomass of <u>Lepidoptera</u> is reduced respectively by 7.6%, 14.1%, 4.2%, the biomass of <u>Coleoptera</u> - by 5.7%, 13.7%, 3.3%, the mass of Hemiptera - by 2.6%, 3.5%, 2.2%, that of <u>Tenthredinidae</u> by 5.0%, 8.7%, 0%, the biomass of <u>Orthoptera</u> - by 0.18%, 6.6%, 2.1%, that of <u>Homoptera</u> - by 0.9%, 2.3%, 0.6%, the biomass of terrestrial molluscs is reduced by 16%, 2.5%, 0.6%. The birds also reduce the biomass of rodents (by 13.6-37.0%).

As shown the phytophagan consumption by birds in azonal forest ecosystems is more than in zonal ones (Inosemtsev, 1978). By isolation of sample trees from birds, it was shown that in oak woods and floodplain oak forests, birds can reduce green mass losses, caused by phytophages, by 25-26% and stem - growth losses by 16-18%, in pine forest - by 17.5% and 6.8% respectively. In areas with dense bird population (oak forests) the reduction of losses can be 3-3.5 times higher.

ON PHENOTYPIC VARIABILITY OF CLUTCH SIZE IN A
POPULATION OF THE MEDDOW PIPIT (<u>ANTHUS PRATENSIS</u>)
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120 clutches of 5 and 6 eggs each (seven clutches of 4 and 7 eggs were left out) and the weight of nestlings of 104 broods were observed on the Aynovy Isles of the Barenz Sea in 1972-1980.

Proportion of 5-egg clutches varied from 18.2% to 64.7% (M+m = 39.4+8.4%; n = 6 years). The mean number of nestlings from 6-egg nests varied from 4.9 to 5.6 (M+m = 5.24+0.13; n = 5 years), from 5-egg clutches - from 4.0 to 5.0 (M+m = 4.52+0.26; n = 5 years). The weight of nestlings before leaving the nest in 6-nestling broods (n = 31) made up 17.8+0.16 g, in 5-nestling broods (n = 43) - 17.28+0.21, in 4-nestling broods (n = 30) - 17.43+0.22.

If the clutch size is hereditable, the more fecund genotype should out the lesser the fecund one. In the present case the 6-egg clutch is more productive,

though on the average more than one third of clutches are less viable; 2) seasonal conditions which make the smaller clutch more productive are repeatedly by more frequent; 3) rearing of a larger brood adversely affects the parent's breeding success; 4) influx of less fecund immigrants is high; 5) part of genetically "6-egg" breeders lay a smaller clutch.

Hence, it might be concluded that: 1) weight, if considered a viability index, is higher in nestlings from larger broods; 2) the large clutch was found more productive in each of the observed seasons; 3) variation in expenditure energy spent by parents on rearing 5-nestling broods or 6 ones is almost negligible as is indirectly indicated by a greater weight of nestlings from larger broods; 4) immigration of less fecund genotype is not to be fully excluded but it can hardly be intensive enough since the areas with the dominating 5-egg clutch are remote in distribution.

All the data afford a conclusion that a considerable part of 5-egg clutches in the area are phenotypic modifications of various kinds.

## ASSORTATIVE MATING IN COMMON TERNS, STERNA HIRUNDO

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I studied Common Terns on Great Gull Island, Long Island Sound, New York, USA. Although male and female Common Terns are almost identical, males tended to have larger bills than females. In 99% of pairs examined the males had larger bills than their mates. Furthermore, they mated assortatively: large-billed males mated with large-billed females and small-billed mated with small-billed females. This may be important genetically because bill size is highly heritable.

## FOOD NICHE SEGREGATION IN THE GREAT REED WARBLER, ACROCEPHALUS ARUNDINACEUS AND THE REED WARBLER, A. SCIRPACEUS IN HUNGARIAN REEDBEDS

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The prey composition, prey size distribution, and feeding microhabitats were analysed in Acrocephalus arundinaceus and A. scirpaceus at three reedbed sites in Middle Hungary, by observation of the adult searching for food and neck-collaring the young.

The Great Reed Warbler carried more variable food items to the young both by species composition and size distribution and searched for food in more microhabitats than the Reed Warbler. There was a small overlap between the two species in all aspects and sites studied.

The food of the Reed Warbler was more similar at the three sites while the Great Warbler had very different food items and microhabitat distribution. There was a clear segregation between the two species at the sites of coexistence.

CORRELATION BETWEEN FREQUENCY OF WING FLAPS AND FLIGHT
VELOCITY IN THE GREY HERON (ARDEA CINEREA L.)

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Most attemps to establish correlation between wing flaps' frequency and
flight velocity for various bird species have not proved successful so far
(Sohnell,1974).

Correlation between flaps' frequency and flight velocity in the grey
heron (Ardea cinerea L.) was studied. Inside the breeding colony during clam,
wind-dead weather flight velocities were measured with the help of a trian-
gular device (Cvelych,1978). Number of bird's flaps on flight within the ob-
servation strip were counted. Since it was found that the flight velocity of
birds en route away from the colony to feed was statistically different from
that of a bird flying back home after feeding, the obtained data were treated
separately.

The graph showing the heron's flying velocity in relation to its wing
flaps' frequency is "V"-like, with a saturation point at the greatest speeds
(correlative ratio r = 0.92; P > 0.001). The flaps' frequency was the minimal
(2, 3 cycles p/s) when the velocity was 39.7 km/h en route away from the co-
lony, and 40.3 km/h in the opposite direction.

Hence a conclusion can be drawn that for the heron there might exist a
flying regime with the minimal energy expenditure (i.e. when the flaps' fre-
quency is minimal) but the optimal flying velocity. This seems to agree with
the data obtained by other researchers (Ryden,Kallander,1964;Kuzmin,Surbanov,
1978).


ACOUSTIC DIFFERENTIATION IN THE YELLOW WAGTAIL-
COMPLEX (MOTACILLA FLAVA SSP.)

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Acoustic signals from various study-areas (South France, South Spain,
North Italy, Yugoslavia, Bulgaria, Rumania, North Greece, Austria, Switzer-
land, FRG, GDR) are compared (sonagrams). There is a clear cut call-note dis-
similarity: southern subspecies (feldegg, cinereocapilla and iberiae) have
·thrill-call-note-types, whereas central and northern palearctic subspecies
(flava, beema and thunbergi) have homologous non-thrill-call-note-types.
Southern subspecies have song-types, which are missing in flava, having only
one song-type. Sonagrams of song-elements were measured. Though partly sig-
nificant there is wide overlap. Yet it can be shown by a discriminant-analy-
sis, that there are two differentiated groups: flava on one hand and the
southern subspecies including hybrid-populations on the other. Subspecies-
grouping by acoustic data makes much more sense in this case than the prev-
ious museum-studies. There is less inter-group hybridization than within
these two subspecies-groups. Moreover there is no more patchy distribution
of subspecies-groups, like there has been in former taxonomic revisions.
Juveniles of flava utter a thrill-call-note type, which might suggest,thrill-
call-notes being the elder. In those intergradation-zones where few hybrids
(20-30%) occur (flava x cinereocapilla x feldegg in the Alps and in Dalmatia;
1090

flava x feldegg in East Yugoslavia and Rumania) there is bilingualism in regard to thrill- and non-thrill-call-notes, no intermediary types exist. This bilingualism is restricted to southern phenotypes and hybrids with flava, but is lacking in pure flava-phenotypes. In the Camargue (South France) where flava and cinereocapilla hybridize (73% hybrids) there is an intermediary call-note-type. This intermediate pattern is regarded as a product of hybridization. Considering that there is influence of learning, it is suggested, that the fixation of used call-note-types within the respective populations is a question of phenotype frequency (ratio parentals: hybrids) or the social or sexual position of potential tutors.

TERRITORIAL BIRD GROUPINGS AND COMPONENTS OF
ANTHROPOGENIC LANDSCAPE
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Formation of territorial bord group-populations (TGP) is affected with some regularity, by anthropogenic landscape components (CAL). Among the CAL, railway and motorcars are most common. Because of it, and also because of all sorts of linear extensions (such as power transmission lines, gas pipelines, etc.) that go along the rail and motor ways, they play an important part in forming birds' TGP all over the USSR. Thus, rail and motor ways may serve a suitable model for establishing any regular effects that CAL may have on birds' TGP.

Both the qualitative and the quantative compositions of natural birds' TGP are affected by CAL. The greater is the saturation of CAL, the more striking, as compared to natural conditions, is the contrast they create, the greater are their effects in either expanding the existing ecological possibilities or creating the new ones.

For instance, in the steppe zone jackdaws, rooks, magpies and some other species nest in forest strips and on power bearings. In the forest zone the same CAL are insignificant; if there are no forests, the jackdaw nests in bridges, roof recesses in stone building, etc. Thus CAL affect the formation of birds' TGP in many various ways depending on the nature of the zone observed.

TROPHIC RELATIONS AND BIOCENOTIC ROLE OF BIRDS IN TUNDRA
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Out of 64 bird species populating Yamal, seven species are planteaters, five eat vegetative parts of plants, though not very regularly yet, five are berry-pickers, ten eat seeds. Speaking of cornivores as birds' feed, lemmings are eaten by nine species, microtines - by seven, willow grouses by five, ducks - by five, shorebirds by six, passerines by eight and fish - by eight. Speaking of insects as birds' feed, longlegs are eaten by 35 species (with 16 out of 35 species consuming them in great numbers) flies - by 27 species (with 10 in great numbers), chiromids - by 23 species (with 14 eating them abundantly) ground beetles - by 23 species (with 3 - in great numbers), teathredines larvas - by. 13 (with 5 in great numbers), anarchnes -

by 15 (with one speecies vsry actively), triphopters - by 17, staphilinids - by 16.

Over 1 ha of water surface in the summer months of different years birds consumed from 5 040 to 15 330 kilocalories, while over 1 ha of tundra onground insectivorous consumed from 3 300 to 8 100 kilocalories. In spring their intake of momentous insects' supply for the 24 hours was 0.5-0.6%, in summer - 1.5-1.7%, in early autumn - 0.4-0.7%. The total decrease in birds' prey is slight, for longlegs it is 1.3% of the supply, for chirono-mids - 0.4%, for arachnes - 4.7%, for tenthredins larvas - 2.4%, for lepi-dopterous larvas - 6.3%. Consumption was not even over the whole territory, it was quite random, when in some parts prey was consumed by half or more. Birds' energy expenditure came up to 0.3-0.6% of all animals' energy over tundra. The role of birds in tundra's ecosystems embrace the quantitative re-gulation of birds' population and the regulation of the energy role of un-dertrophic levels. Moreover, birds transfer from water to land 2.5 kg/ha (damp weight) of organic substances.

SHORT MIGRATORY MOVEMENT OF ROBIN IN CAMPANIA, ITALY

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Erithacus rubecula rubecula is found in Campania, where it is considered to be a permanent resident. However, it undertakes regular migrations re-lated to its annual cycle. It prefers to winter in open fields and along the shore and to breed in mesophilic areas. The short migrations, which usually terminate on the inland appenninics (mountains), follow routes that take advantage of rivers liks the Sele and the Volturno, of the Lattari or Aurunci mountain chains, or of narrow valleys between the Picentini and Al-burni mountains. The major breeding sites are localized in the Matese, Lat-tari, Picentini and Alburni mountains. The migratory routes were studied, through repeated capture of individuals, beginning from Vivara Island, through the Gulf of Naples and towards Partenio, Camposauro and the Matese mountains. A faunistic inversion was observed in the mountains near Naples due to the peculiar microclimate character of this area; the Robin breeds at the bottom of the Astroni Crater and usually passes the winter months along its top. We have tried to differentiate the migrator of heterogeneous populations through an ornithomstric analysis.

BIRDS RESOURCES OF THE YOUKON-KUSKOKWIM DELTA, ALASKA

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The Yukon-Kuskokwim Delta comprises an area of approximately 69160 $km^2$, 400 kilometers north to south and 320 kilometers east to west from 60° N to 63° N latitude and 160° W to 163° W longitude. Low, wet sedge-grass meadows supporting numerous waterfowl and shorebird spscies, in high densities, do-minate the coastal fringe habitats. Lichen-ericaceous tundra prsdominates at interior and more elevated locations. The avifauna of the vegetated inter-tidal zone, ths low coastal frin affected by maximum storm surges, supports

1092

the broadest composition of nesting species and higher overall densities than all other habitats on the delta. Approximately 49 species nest within the vegetated intertidal zone, 36 of which also occur in other delta habitats. Twenty-four species are known to nest only in habitats other than the vegetated intertidal zone. Small tidal sloughs and tidal rivers numbering 1933 and 153, respectively occur within the 8942 $km^2$ area of vegetated intertidal. These water bodies in addition to 27 lagoons provide essential molting and feeding areas for 22 species of waterfowl and 21 species of shorebirds. A total of approximately 100 species of birds occur regularly as both spring and fall migrants on the Yukon-Kuskokwim Delta.

## GENTOO PENGUIN ECOLOGY
Bernard Despin

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The Gentoo Penguin breeding cycle has been studied in two breeding localities: Crozet Islands (ile de la Possession) and South Orkney Islands (Signy Island).

The Gentoo Penguin is to be seen everywhere on the Islands but it is never abundant.

Egg and chick mortality is very high on Crozet and less important on Signy (1976-1977) but it is sometimes catastrophic (South Georgia 1978). Chick rearing, bird size, food and call have been compared in both populations.

At attempt is made to explain the wide geographic distribution of the species in relation with the ecological data.

## ACTH AND BEHAVIOUR IN DOMESTIC PIGEONS
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Extensive studies performed on mammals have clearly demonstrated that in several species, various peptidic hormones, and namely adrenocorticotrophic hormone or ACTH, exert an important modulatory influence on behaviour.

Up to now, however, the possibility that ACTH directly influences the behaviour of non-mammalian species, and especially of birds, has been poorly investigated.

We studied this problem in the domestic pigeon.

ACTH was administered either peripherally (into the pectoral muscles) or centrally (into the cerebral ventricles).

The influence of the hormone was researched on one hand on "displacement activities" such as yawning, headshaking or preening, and on another hand on conditioned behaviour.

Positive data were obtained, showing that ACTH induces shortterm effects (appearing within minutes after an injection) on some behavioural patterns.

Important qualitative differences between results obtained in mammals and in pigeons were also observed.

These differences will be discussed. They point out to the possibility that the endocrine regulation of some aspects of behaviour differs in birds and in mammals.

DEVELOPMENTAL FACTORS IN BIRD BEHAVIOUR DURING
EARLY POST-EMBRIONAL ONTOGENESIS

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Study has been made of the relationship between the complication in the organisation of natural behaviour of 4 birds'species (Ficedula hypoleuca, Parus major, Phoenicurus phoenicurus and Cuculus canorus) and the whole complex of ecological factors underlying the steady environment in the early post-embrional ontogenesis. It has been shown that at an early nestling stage only feeding behaviour appears to be formed. Thus before nestling's eyes are open, it is governed by acoustic stimuli, i.e. by wide spectre sounds arranged in mechanical succession (the bird makes noise with its feet, disturbs the nest, produces a specific "feeding" call). The passive defensive response appearing at the beginning of the second half of the nestling period (the bird becomes apprehensive) is controlled by rhythmically arranged alarm calls with narrower spectre sounds compared with a "feeding" call. Finally the behaviour directed by species song appears at a later nestling stage. The rhythmical and structural complication of the above signal is accompanied by the narrowing of the frequency spectre. In the post-blind period the modality of starting afferentation of feeding behaviour changes which is now induced by diffusive change in lightning, the latter being caused by the parental shape in the nest hole. At the end of the nestling period food-obtaining response is induced and directed by the moving silhouette of the bird. The involvement of the organised visual environment in the ontogenesis of the goal-directed behaviour suggests the existence of the corresponding visual experience acquired during specific for each type periods of development.

Thus the complication of the acoustically and visually directed behaviour is typical for all the investigated species of nestlings in early post-embrional ontogenesis. It is accompanied by parallel strengthening of controlling signal patterns. The gradual steady complication of sensory mechanisms and forms of behaviour directed by them is connected with the growing requirements for the perception of the environment which becomes more and more complicated.

DYNAMICS IN THE VARIABILITY OF MORPHO-PHYSIOLOGICAL INDICES
IN BIRD ONTOGENESIS

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Changes in the values of variation coefficients in the relative weights of heart, liver, pancreas, brain, locomotory and stomachic muscles, adrenal glands, and relative bowel and caecum lengths during growth and development were studied on birds of 50 species. A distinct inverse correlation between the functional importance of each organ and the amplitude of its relative size variability was examined. Variation coefficients of the heart and the

relative weights of the flight musculature were significantly greater in the
embryos than in the young and the adults. This indicates that during the ac-
tive life span of the bird (i.e. genetical diversity is disguised by pheno-
typic variability) gradually individual, genetically determined changes in
these organs were smoothed away. The reverse phenomenon was observed in index
changes in liver with age: for the embryos as compared to the young (generi-
cal diversity is strengthened by phenotypic variability) variation coeffi-
cients were much lower.

DIFFERENCES IN THE FINE NEURONAL STRUCTURE
OF CERTAIN BRAIN SECTIONS IN CROWS AND PIGEONS.
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Study of fine neuronal structure of paleostriatum, neostriatum and hyper-
striatum ventrale in crow and pigeon brain was carried out on histological
preparations by Golgy method. The differences manifested themselves in the
increased area of cellular-dendritic fields, the increased number of dendrit-
ic endings and a denser cover of protoplasmic protrusions in neostriatum and
hyperstriatum ventrale as compared to paleostriatum. The complication of the
neuronal structure might determine greater functional capacity of neostriat-
um and hyperstriatum ventrale as compared to that of paleostriatum.
Differences in the fine neuronal morphology have been observed between
the analogous neuronal groups in crows, possessing a great capacity for ex-
trapolation and in pigeons deprived of it. As compared to pigeons the crow
paleostriatum, neostriatum and hyperstriatum ventrale neurones are morpholo-
gically finer: the dendrites are thinner, more sinuous and are provided with
a denser cover of extremely fine protoplasmic protrusions. A more ingenious
neuronal structure apparently sets up morphological prerequisites for es-
tablishing a greater number of contact junctures and, probably, for finer
analysis and processing of information by these brain regions in crows than
in pigeons, which may contribute to crows' greater capacity for extrapolation.

CORRELATION OF COPPER, LEAD AND ZINC MAINTENANCE IN
PLUMAGE OF SOME BIRDS
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Satiation of biosphere with metals is one of the most important problems
of environmental pollution. United Nations Interdepartmental Group on mo-
nitoring has listed lead, mercury, cadmium, copper as pollutters to be given
primary attention.
The essential condition for pollution control is in establishing regional
norms of natural content of these metals since technogenic pollution is
higher than the natural content, the latter due to its geochemical origin
sometimes being locally anomolous.
In search of bioindicators sensitive to the concentration of heavy metals
in natural environment by spectroscopy we examined metal content in the feat-
hers of some bird species over different areas of the USSR European part.

Direct correlation between lead and copper content in the plumage (r=0.30, p ∠ 0.05) was established, though no correlation was found for zinc and lead or zinc and copper. Knowing the copper content, which is easy to detect, one can predict the lead content in the plumage.

THE GREAT BUSTARD (OTIS TARDA) POPULATION AND CONSERVATION
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The Great Bustard (Otis tarda L., 1758) is an endangered species. The western palaearctic subspecies (O.t.tarda) is estimated at about 17000 birds (1980), the east Asian subspecies (O.t.dybowskii) amount to more than 3000. The western distribution centres are in the USSR (7000), Hungary (3400), GDR (500) and also Spain (more than 4000 birds). The decrease in the whole breeding area is reflected in the population decline in the GDR from 4000 (1940) to 500 birds (1980). Conservation management is necessary. The Great Bustard is internationally protected by CITES. In the GDR there has been no shooting since 1949, protection by law as an endangered species (1955) and establishment of a special conservation programme (1971). In 25 State Bustard Protection Areas (80 000 ha), there are protection of display and nest sites, cultivation of Brassicaceae etc. Between 1968 and 1980, 240 young bustards from disturbed clutches were hatched, hand-reared to adult size, ringed and released in the wild. Since 1978, released females have been bred successfully. Several times those ringed birds returned after migrating more than 500 km from wintering grounds in the Netherlands.

DER SCHUTZ DER WEINBERGE UND AGRARROHRSTOFFE VON
VÖGELN IN USBEKISTAN
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**Innerhalb** 3.5 Monaten schädigen die Vögel den Weinbergen in Usbekistan. Im Juli werden die frühreifenden Sorten der Weintrauben von turkestanischen Staren, Mainen, indischen Sperlingen, Feld- und Weidensperlingen geschädigt. Im August sammeln sich in den Weinbergen auch Dohlen und westasiatische Elstern. Im September-Oktober werden die spätreifenden Sorten der Weintrauben von turkestanischen Staren, Felsperlingen, Dohlen und Elstern geschädigt. Der Schaden beträgt 20-25%. Um 10-20% werden Kernfrüchte, Getreidekultur und Feige **geschädigt.** Es wurden Vergrämungsmassnahmen ausgearbeitet: akustische Repellents und optische Reizmittel (Spiegelkugeln). Effektiv sind Alarmsignale von Mainen und Rufe des Baumfalkes. Die Spiegelkugeln werden auf 2.5-3.0 m hohen Stangen gestellt (6-8 Stück auf 1 Hektar). Das vermindert den Bestand der Vögel auf landwirtschaftlichem Gelände um 60-90%.

ROLE OF ENVIRONMENTAL STIMULI IN REGULATION OF ANNUAL
CYCLES OF PROLACTIN SECRETION IN MIGRATORY AND
SEDENTARY BIRDS

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Amplitude of diurnal fluctuations of pituitary prolactin content indicating the intensity of prolactin secretion was studied in the migratory Chaffinch and the sedentary House Sparrow during the year. In the Chaffinch increase in diurnal fluctuations occurs from April to October and coincides with productive phases of the annual cycle. In winter and in pauses between seasonal events, pituitary prolactin content decreases and its diurnal fluctuations disappear. In the House Sparrow seasonal variations of the amplitude of fluctuations are similar to those in the Chaffinch. Differences between the two species relate to the pattern of diurnal rhythm of pituitary prolactin in migratory periods.

Amplitude of diurnal fluctuations of pituitary prolactin in every seasonal state (with the exception of the pauses) correlates with daylength. Experiments with different photoperiodic regimes in winter and in summer also confirm that the amplitude is mainly conditioned by photoperiod. However decrease of the amplitude in.transitional periods between seasonal events indicates that other factors (perhaps endogenous) may influence the intensity of prolaction fluctuations.

Another environmental stimulus affecting pituitary prolactin content is temperature. Low temperature in winter has been shown to cause an increase in diurnal fluctuations of pituitary prolactin in Chaffinch.


INTERCHANGE OF HELMINTHS OF WILD BIRDS AND
POULTRY IN KAZAKHSTAN

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Definitely marked community of helminth fauna of wild and domectic Galliformes and Anseriformes was determined as a result of the studies carried out in Kazakhstan. Undoubtedly it shows the interchange of helminths constantly taking place between them. It is known that about 20 helminth species are pathogenic to domestic fowl and turkeies parasite in wild Galliformes (quail, grey partridge, pheasant etc.). More than 50 helminth species infecting domestic ducks and geese were recorded for wild waterfowl. There is a definite ecological chain providing helminth interchange of wild birds and poultry and arising now and then of epizootics of helmithosis among domestic fowls, ducks and geese. Helminth fauna interchange of wild birds and poultry is also conditioned by historic factors. Conditions of domesticating and the period from the beginning of domesticating of birds were of considerable importance.

Along with constant selection of poultry,selection of their helminths due to definite signs inevitably took place. It caused appearance of new helminth forms adapted to the hosts and to the conditions of their keeping changed in the process of domesticating.

## BIOLOGICAL INTERPRETATION OF AVIAN SKULL MORPHOLOGY

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Method of functional analysis based on morphological description draws on the physical laws underlying the mutual matching between the bone-muscular construction on the one hand and the ecological properties of the species on ths other. The skull is to be analysed as a complex bony system together with the ligaments and muscles as part of the whole feeding apparatus (jaw and tongue apparatuses). Methods of fundamental mechanics allow one to establish the mechanical properties of the morphological system which clearly determine its functional potentialities, and in this way afford the recognition of the biological (e.g. ecological) aspects of skull structure. The examples we used as illustrations are related to the significance of various cranial features such as the "hyoid" horns, lower and false upper jugal arches, schizognathous and schizorhinal conditions of the upper jaw and the structure of some quadrate articulations.

## THE EFFECTS OF MILITARY JET OPERATIONS
## ON NESTING BIRDS OF PREY

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During the 1980 and 1981 field seasons, data were gathered at more than 40 breeding sites of 10 species of raptorial birds in an effort to record responses to low level jets and sonic booms (or simulations). Severe negative responses were occasionally observed. Most often adults and large young were merely alerted or alarmed by the stimuli. Young falcons tended to flee deep into ths eyrie in response to nearby jets. No eyrie abandonments or reproductive failures were attributed to the jets or booms during the study. Eyrie reoccupancy rates were considered normal for sites tested one ysar and checksd for occupancy the next.

## FEEDING ECOLOGY OF THE NIGHT HERON NYCTICORAX NYCTICORAX
## IN RICE FIELDS

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A dense population of herons (especially Night Herons, about 12.500 nests in 1981) breed in about 5.000 $km^2$ of Northern Italy in an area with few natural marshes but with intensive rics cultivations. Rice fields, more uniform and more easily obssrvable than most natural acquatic habitats, are very suitable for studies on the ecology of wading birds.

In our study area (near Pavia), the main prey of Night Heron during nestling period are amphibians, 60.3% (in numbsr), and fish, 69.4% (in dry weight). Herons capture their prey in rice fields 60-70% (no.) or 30-60% (d.w.); a major prey item is tadpolss which are abundant at the time when the nestlings are growing and have higher food requirements.

Observations made during the full daily cycle (at night with light intensifiers) showed that in nestling period, the Night Heron has a uniform

1098

activity rhythm, with a higher daytime food intake, when more tadpoles are taken. From these data and from the energy content of prey and the expenditure of each activity I calculated the mean energy intake of an adult as 460 kcal/day, or 112% of its expenditure plus that of the nestlings.

The dispersion of the Herons to feeding grounds was significantly clumped, and the degree of aggregation varied in relation to patchiness of the prey, supporting the view that herons use other individuals as indicators of good foraging sites. During foraging flights, herons do not leave the heronry randomly in time and in flight directions, which supports the hypothesis of the colony as an information centre. They alight near plastic models of feeding herons in poor feeding sites, so they also locate food sources by virtue of seeing other birds feeding.

## MORPHOPHYSIOLOGICAL MECHANISMS OF CERTAIN COMPLEX FORMS OF BIRD BEHAVIOUR

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The lesion of the archicortex and the Wulst (striatum section progressively developing in the class of birds) was attempted to determine the sections in bird brain responsible for the functions performed by the new cortex in mammals. Influence on the following experimental models of elementary reasoning ability was studied:

a) the ability to extrapolate the direction of a food irritant, withdrawn from the field of vision, - in birds with an average (chicken) and high (Corvidae) level of reasoning ability;

b) the ability to operate the dimensions of figures obtained empirically - in birds with a high level of reasoning ability (Corvidae). It was demonstrated, that the removal of the Wulst brings about behavioural changes common to both species in performing extrapolation tasks; more specifically, it increases the incidence of failures accompanied by disorderly movements about the cage. The fact confirms the involvement of the Wulst in the construction of complex eyesight-controlled motory acts programm (Morenkov, 1975). It was also found that after the operation chicks retain the characteristic prevalence of correct solutions (turning round the screen at the right side) during numerous task presentations (Zinovieva,1975). In contrast to chicken, Corvidae lost the ability to extrapolate. In case of experienced birds, the incidence of correct passages decreased, even though it exceeded that of the incorrect ones. Experimentally naive birds lost their ability to extrapolate even in simplified experimental situation (shortened acreen). In contrast to this, the ability to operate empirically-obtained dimensions of figures was not impaired, in spite of the lesion of the Wulst.

The data so far received suggest that the structural basis of **reasoning** ability in birds varies according to:

a) the level of its development in different species (Corvidae, chick, chicken);

b) the form of reasoning ability specific to birds of a particular species.

## VARIABILITY OF PLUMAGES IN THE SLATY BLACK-BACKED GULL LARUS SCHISTISAGUS, STEJNEGER

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Analysis of a series of 120 specimens (of which 63 were collected by the author at Geka Bay, Olutorski District, Kamtschatka Region in 1976-77) of Slaty Black-backed Gulls of different ages showed that: (1) A clear boundary for plumages is not observed in all individuals. For the third nuptial plumage, 1 bird (of 11) had pure white rectrices, and for the fourth nuptial plumage, 8.7% of the birds (of 57) had remnants of brown coloration on these feathers. (2) In the fourth nuptial plumage, decreasing brown coloration on the feathers of the tail and the wings is independent to a considerable extent. Birds with brown coloration of the rectrices may have the definition coloration of the wings, and on the contrary, individuals with pure white tails may still have the brown coloration on the wings developed to a maximum amount. Irrespective of the coloration of the rectrices, a gradual transition exists from maximum to minimum development of brown coloration on the wings. (3) The definitive coloration of the rectrices appears as early as the fourth non-nuptial plumage in 92% of the individuals and the definitive coloration of the wings appears only in the fifth non-nuptial or fifth nuptial plumager in 98.3% of the birds. Therefore, the principle criterion of differentiation of the fourth and fifth plumages should be the coloration of smaller feathers of the wing (rudimentary primary, distal major primary coverts, feathers of the alula and minor secondary coverts), not the coloration of the rectrices as was accepted earlier (Firsova, 1975).

## NESTLINGS' CONTROL OF LOCOMOTION REACTIONS BY ACOUSTIC SIGNALS

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Our purpose was to study control of locomotion of nestlings under conditions of game-breeding farms by using "acoustic traps". 9 species of maturonal birds (Anseriformes, Galliformes) were observed. During the experiments records of different acoustic signals of the nestlings, females and their monotonal imitators were produced to the experimental groups of the same nestlings. The results of experiments showed that: (1) It is possible to use the juvenile contentment sounds, call-sounds of the female and monotonal signals in the specific ranges of frequencies as the acoustic attractants if these signals were first presented to the nestlings during the "critically-sensitive"period. (2) The hatch of nestling may be attracted to an immobile "acoustic trap" only in a distress biological situation. (3) In comfortable situations it is possible to direct the nestling movement by using mobile loudspeakers only. (4) The acoustic attractants retain their influence until the birds are one month old. (5) The acoustic attractants can be used in game-breeding and poultry-breeding for getting the nestlings together and for transferring them in a given direction.

COMPARATIVE FORAGING EFFICIENCIES OF SELECTED AVIAN
FRUGIVORES

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While the different foraging methods of avian insectivores have been
studied extensively, relatively little attention has been directed toward
the foraging behavior of frugivores. In this ongoing study, I am examining
the feeding methods of more than twenty species of birds that exploit fruits
of Allophyllus guaraniticus (Sapindaceae) either opportunistically, or as a
primary food source. This tree, a common component of the forests of eastern
Paraguay, has fruits ranging from 7 to 10 mm in diameter. Observations are
being made of birds in the field and in captivity. Particular attention is
being paid to the manner in which the fruit is removed from the branch, the
way the bird manipulates it in its bill, and the method by which the pulp is
separated from the single, large seed. The way in which these tasks are per-
formed is determined in large part by the size of the bird's gape relative
to fruit size. Efficiencies of pulp removal by birds using different methods
has been measured, and allows for an evaluation of these methods in terms of
optimal foraging strategy.

POPULATION ANALYSIS OF SARDINIAN WARBLER IN THE VIVARA
ISLAND (MEDITERRANEAN SCRUB)

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This work presents an analysis of certain ecological aspects of the Sar-
dinian Warbler (Sylvia melanocephala), which is particularly adapted to the
arid climate of Mediterranean islands.

The preference of habitat and distribution of the species were studied
mainly by employing the index of diversity (H). An analysis of stomach con-
tents of accidentally killed specimens and a study of other competing species
(Robin, Blackcap, Hedgesparrow, Chaffinch) in the area enabled us to compre-
hend better its niche and feeding habit. This species is mainly insectivorous.
Fecal material, song and courtship behaviour were also studied, always in
relationship to the characteristics of the scrub ecosystem. Capture and re-
capture of ringed individuals were used to study population dynamics. Brief
spring migratory movements were observed; in this period migratory individuals
outnumbered the local population.

Finally study of the structure of local population was complemented with
ornithometric tables. The life span of the of Sardinian Warbler is 3 years.

THE URBAN AND SUBURBAN AVIFAUNA IN HOKKAIDO, JAPAN

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A study of the urban and suburban avifauna during the breeding season was
conducted in relation to vegetation cover in Obihiro, Hokkaido. The number
of bird species observed increased as the percentage of vegetation cover in-
creased, and the relationship between the number of bird species (Y) and

percentage of vegetation cover (X) is: $Y = 4.1744 + 0.3542X - 0.0020X^2$. Species diversity increased from areas with low percentage of vegetation cover to areas with high percentage of vegetation cover, and was highest in woodlots and grassland.

FEEDING STRATEGIES OF THE ARCTIC SKUA AT FOULA,
SHETLAND, UK

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The feeding behaviour of Arctic Skuas nesting on Foula was studied in 1976, 1978 and 1979. In each year the skuas host preferences varied between Puffin and Arctic Tern for different reasons. In 1976 the preferred host was the Arctic Tern, in 1978 the Puffin and in 1979 the skuas switched from Arctic Terns to Puffins. Interpretation of these results suggested that when a choice is available, Arctic Skuas behave as would be predicted by optimal foraging theory, but that this choice is not always open to them. The host preferences on Foula largely depend on the relationship between Arctic Tern breeding success and the balance between the size of sandeels carried by Arctic Terns and by Puffins. Foula is the largest colony of Arctic Skuas in Shetland because of the availability of two alternative hosts, and the ease with which courting Arctic Terns can be exploited close to the colony early in the breeding season. These options are not present at other Shetland colonies.

BEHAVIOURAL PHYSIOLOGY OF WILLOW PTARMIGAN (L. LAGOPUS LAGOPUS)

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I have used heart rate (EKG) telemetry to monitor behavioural influences on the physiology of female ptarmigan, incubating or free ranging. I have recorded abrupt and extensive changes in heart rate from a variety of external stimuli. Threatening stimuli such as calls and sight of predators, fear calls of other animals or the approach of humans, inevitably caused strong and persistent bradycardia. Exciting stimuli, like the territorial call of a hen's own cock or startling noises, caused shortlasting tachycardia. When the startling noise was followed by a threatening stimulus, for example when a man signalled his approach by breaking a branch, tachycardia was quickly followed by bradycardia.

The time course of these responses was characteristically subject to habituation. Repeated provocations of wild, incubating hens by human louds caused a progressive lessening of the behavioural and physiological response. Hens incubating close to human settlements showed weaker responses than those breeding in remote areas. Hens incubating in captivity where they are continuously exposed to human activity during the daytime, show little bradycardia. Typically, however, their heart rate decreased if disturbed during the night. We conclude that heart activity is a sensitive indicator of the emotional status of the bird, integrating recent history with present stimuli.

## STRUCTURE OF POPULATIONS AS INDICATOR OF
## DYNAMICS IN THE NUMBER OF GALLIFORMES

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2610 Tetrao urogallus, 1235 Lyrurus tetrix, 8097 Tetrastes bonasia, 2705 Lagopus lagopus and 3010 Perdix daurica have been examined over a number of years to establish changes in the populations of wild Galliformes related to dynamics of their number. Figures for sex correlation in Tetrastes bonasia populations point to the evident and constant prevalence of cocks (1:1.39) and subadultus - 69.3%. The number of adult cocks and young hens is subject to the deepest changes. When the size is lower, the number of adult cocks is greater while the number of young hens falls down sharply. The decrease of the Tetrastes bonasion is indicated by the decreased number of young birds (below 60%). There is a direct correlation of the number in the annual increase to the number of young crebs in the populations of Tetrao urogallus and Perdix daurica. The analysis of data on the Lyrurus tetrix population structure shows a considerable increase of a number of young hens along with the total increase of bird's number.

In the years of high quantity of Lagopus lagopus and its intensive migration to forest-tundra, cocks and subadultus considerably increase (cocks about 60%). Bird migration is sex-different. Hens are the first to go and to the farther distances. Thus among the species of Galliformes, examined by us, with the exception of Lyrurus tetrix, the phase of quantitative increase is characterized by the increased number of cocks and young birds in their population structure.

## COMPARATIVE ANALYSIS OF THE ROUGH-LEGGED BUZZARD
## POPULATION PARAMETERS ON TWO SITES OF TUNDRA WITH DIFFERENT
## DEGREES OF ANTROPOGENIC INFLUENCE

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37 breeding territories of the Rough-legged Buzzard were found near the town of Vorkuta and the neighbouring miners' settlements which are arranged in a circle called the Vorkuta Ring (V.R.) in the north-east of the European part of the USSR during the field seasons of 1979 and 1981.

Observations were conducted mainly on two sites of tundra: 1. Site I subject to industrial pollution, construction of the transmission electric lines (TEL), pasturage of cattle, recreation, etc. This site (about 120 sq km) includes the area inside the V.R. and some 5 km outside it. 2. Site II - relatively natural tundra environment (about 60 sq km).

On both sites micro-rodent population peak was observed in 1979 and depression in 1981.

Contrary to what was to have been expected, Rough-Legs' population density in 1971 and 1981 and the breeding success in 1979 appeared to be higher on site I.

|  |  | 1979 |  | 1981 |  |
|  |  | site I | site II | site I | site II |
| nesting density |  |  |  |  |  |
| (pairs/100 sq km) |  | 19.4 | 14.7 | 12.5 | 8.3 |
| breeding success (average |  |  |  |  |  |
| fledgelings/suocessful nest) |  | 4.5 | 3.2 | 1.8 | 2.8 |

The data suggest, that the man-made landscape is likely to possess certain advantages for Rough-legs which, to some extent, make up for the disadvantages of the man-cultivated site. There might be a) comparatively greater abundance of microtine rodents (mainly voles) within the V.R. and their greater vulnerability because of scarce tundral vegetation, especially shrubbery, and its substitution for carex-cereal cover; b) greater abundance of food in early spring, e.g. migrating ptarmigan dashing against the TEL wires. The TEL poles may serve as additional attractions for those raptors as they are suitable perch sites and even nesting sites (5 nests were found on them). Along the TEL Rough-legs showed especially high nesting density of 33.5 (1979) and 18.8 (1981) pairs/100 sq km.

THE BIRDS OF FOREST-PLANTATIONS OF MOLDAVIA
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The dependence of specific and quantitative composition of birds on the quality, structure and age of plantations was determined. No more than 12 species of birds nested in young plantations. The population density was 370 pairs/$km^2$. Larks, Stonechats and Warblers were predominant. In broad, dense middle-age forest-plantations tne population density of birds is 970 pairs/$km^2$; the number of species increases to 24. Warblers, Thrush Nightingale, Shrikes, Golden Oriole  Magpie, Turtle Dove, Greenfinch predominate. The largest population density of birds (1600 pairs/$km^2$) and number of species (42) were found in old forest-plantations with well expressed tiers. Shrub and crown species predominate in this plantations. Hole-nesting birds appeared here. The narrow forest-plantations, with high population density of birds, are characterized by few species of birds.

SEASONAL MIGRATIONS OF LARUS ICHTHAETUS PALL. IN KAZAKHSTAN
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The seasonal migrations of Larus ichthyaetus Pall. were studied at Alakol Lake, Aral Sea, Tengiz and Dzalauly Lake (Kazakhstan). During 1952-1980, we banded 30376 nestlings and received 921 returns. Analysis of the results demonstrated that the spring migration began by the end of February and early March. Adults migrate in shortest time but elongated flight of immatures is finished by the end of April or mid-May. After the fledglings have begun to fly (June-July), the gulls disperse very widely and the  areas of birds from different colonies overlap very much. Over the greater part of Kazakhstan the migration is finished by October and the birds reach winter quarters or

near them in November. The winter quarters are mainly situated in the southern Caspian Sea and inland reservoirs of Iran. Small numbers of Larus ichthaetus stay on the coast of the Arabian Sea, at Tana Lake in Ethiopia, in the delta of Brahmaputra (India) and probably at the Black Sea also. The wide wandering of birds during non-breeding time is an adaptation which provides successful reproduction of progeny under sharp changes of external conditions in the nesting area. The mortality of gulls form 80% during the first year and 50% per annum during the remaining years. The maximum survival is 16 years and 3.5 months.

BIRD COMMUNITIES IN EXOTIC PINE PLANTATIONS IN AUSTRALIA

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In Australia, 860.000 hectares of exotic conifers have been planted on land that was originally native forest. Bird species composition and abundance in plantations has been found to be different from that in native forest and also between silvicultural treatments. The avian community in plantations is dominated by predominantly "opportunistic" insectivorous species, with a paucity of species that feed upon nectar or require hollows in which to nest. These differences are discussed in terms of the: (1) structural uniformity of plantation systems; (2) differences in the availability of food (invertebrates, nectar, pollen) and nesting hollows; and (3) differences between the growth form of exotic conifers and native eucalypts.

The paper reviews the results of comparative studies of birds in pine plantations and eucalypt forests and discusses the implications of forest management options to promote avifauna. Similar options have been generated in most countries establishing plantations, viz.: (1) verying plantation layout to maximize interfaces and age differences; (2) retaining or regenerating corridors of native forest; and (3) providing natural or artificial nesting hollows.

L'HIVER DE LEUCOSTICTE ARCTOA À KAMTSCHATKA

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Il y a 10 ans la plupart des Leucosticte arctoa hivernant à Kamchatka frequentaient la littoral.

A Petropavlovsk les oiseaux apparaissaient au février et quittaient la ville au mois de mars-avril.

Les dernières années des milliers de Leucosticte arctoa apparaissent dans les villes de Kamtchatka avant la neige.

D'octobre jusqu'à mai les Leucosticte arctoa font la partie du paysage anthropogene des chantiers de construction.

Pendant les periodes de l'années dépourvues de neige les oiseaux se nourrissent des semences des mauvaises herbes; en hiver ils se réunissent sur les chantiers de construction sans de neige, ce qui indique le processus de la synantropisation de Leucosticte arctoa.

AGE AND SEX RATIOS OF SOME BIRDS ON THE AUTUMN
MIGRATION IN WESTERN TIEN SHAN

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In the foothills of Western Tien Shan (Chokpack pass) 153246 birds of 14 species were banded during 1970-1979. In the first year after banding, the mortality of adults and yearlings was different in some species (in Hirundo rustica 43.7 and 65.7% correspondingly, in Riparia riparia 55.6 and 63.6%, Corvus cornix 37.5 and 76.5%, C.monedula 39.6 and 56.6%, C.frugilegus 55.9 and 62.6%).

In the most species males predominate, and in Accipiter nisus they formed 52.0% on average, in Streptopelia orientalis 54.6%, Merops apiaster 57.2%, Fringilla coelebs 56.1%, F.montifringilla 60.0%). The highest productivity is recorded in A.nisus, Columba oenas, M.apiaster, H.rustica, R.riparia, Emberiza leucocephala, E. citrinella, C.cornix (1.7-4.2 yearlings: 1 adult). At the beginning of migration the females and yearlings predominate in A.nisus, C.oenas, C.eversmanni, H.rustica, R.riparia. In other species the similar findings were not recorded which can be explained by the different periods of migration of different populations.

The species with similar feeding (H.rustica, R.riparia) have different migration times which can have adaptive significance for the reduction of trophic competition at the flight route.


STABILITY AND SUCCESSION OF THE AVIAN COMMUNITIES IN WOODLAND
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Stability (as constancy and as resistance) of the breeding avifauna was determined for the five phases of the secondary succession of a deciduous forest in Poland. The variability (the reverse of stability) of species richness (S), species diversity (H') and density (N) of the bird communities were mainly analysed. A total variability (directional var. of succession + + random var.) and separately random variability which are independent of successional trends were estimated.

In the first 15 years of succession the directed variability of the features investigated prevailed. In the later stages random variability is of decisive significant. The evaluation of both total and random variability shows that the stability of the bird communities increases in general, with the development of succession yet it need not be the lowest in the initial phase and the highest in the climax phase. These results are consistent with the Odum (1969) general "model" of succession.

Total variability is closely and negatively correlated ($r = -0.9$) with S, H' and N. In other words more dense and more diverse bird communities are more stable. But no causal-effective dependence between these values was proved.

## CLUTCH AND EGG SIZE IN GREAT CRESTED GREBE (PODICEPS CRISTATUS L.) ON DRUZNO LAKE (NORTHERN POLAND)

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The research material of this study consists of over 1500 clutches measured in the years 1976-1980. Significant changes were found in the two parameters of clutch size and egg size during the breeding season. Between-years differences in egg size are smaller and are significant only for years of extreme values. Egg size on Druzno Lake differs from the data reported from some other geographical regions. The other aspects analyzed are the relations of both parameters to the type of nesting (territorialy, colonialy and in Black-Headed Gull colony) and the within-clutch variation of egg size.

## COMPETITION AMONG NORTH KAZAKHSTAN PODICEPS DURING REPRODUCTION PERIOD

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The four Podiceps species making their nests together on the big reed lakes (Podiceps cristatus, Podiceps griseigena, Podiceps nigricollis, Podiceps auritus) are similar in a number of indications: marriage behaviour, breeding spectra, nesting biotopes and main indices of the reproductive cycle. Competition between these species is weakened because of differences in nesting and breeding sites, phenology of reproduction (small species start laying their eggs one or two weeks later than big ones) and also due to the numerical domination of one of the species on every site. Some peculiarities of behaviour such as interspecies' aggressiveness (especially of Podiceps griseigena) during nesting and hatching periods and early roaming of Podiceps cristatus and Podiceps caspicus broods from their nesting places also promote this.

The density of relationship increases under the influence of unfavourable abiotic factors and first of all under the fluctuation of hydrological regime of the reservoirs. Their shallowing alongside with the artificial thinning of brushwoods make the Podiceps griseigena a dominating species. The filling - in of big lakes changes the correlation in favour of Podiceps cristatus. Some reservoirs, favourable for the habitation of all the four Podiceps species, nevertheless from year to year are populated by one of them mainly, most often by Podiceps griseigena - a species of great competative ability.

## INTERACTION BETWEEN TEMPERATURE REGULATION, SLEEP AND CIRCADIAN TIME IN THE PIGEON

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Pigeons show daily fluctuations of body temperature ($T_b$) and arousal state distribution. In is known that: (1) in pigeons, the $T_b$-cycle depends on

diurnal changes in spinal thermosensitivity; (2) hypothalamic thermosensitivity in mammals and spinal thermosensitivity in birds are influenced by arousal state; and(3) in mammals, arousal state distribution is altered by altering hypothalamic temperature.

To study the interaction of temperature regulation, sleep, and circadian time, pigeons were chronically implanted with thermodes and thermocouple reentrant tubes both in the vertebral canal and in the anterior hypothalamus. Arousal states were determined by EEG-, EOG-, and neck muscle EMG-electrodes. Respiratory rate was measured via impedance pneumography; metabolic rate was determined by measuring oxygen consumption.

First, we examined the characteristics of spinal thermosensitivity. At any given time of the light-dark (LD) cycle, the thresholds for penting and shivering were lower during slow wave sleep (SWS) than during wakefulness. Furthermore, these thresholds in both awake and sleeping animals were lower during D than during L, thus supporting the idea that CNS mechanisms controlling arousal states and circadian rhythmicity have separate influences on temperature regulation in the pigeon.

In a second series of experiments we looked at the influence of spinal and hypothalamic temperature on the distribution of sleep states during D: slight warming of the hypothalamus to a level characteristic of L had little or no effect. Warming the spinal cord, however, increased the amount of SWS, nearly abolished paradoxical sleep, and, moreover, produced a sharp decrease in body temperatures. Since birds exhibit high spinal thermosensitivity, but not the hypothalamic thermosensitivity characteristic of mammals, our results support the hypothesis that thermoregulatory conditions have a strong influence on the distribution of sleep states.

DISTRIBUTION OF BREEDING SITES AND THE NUMBER OF SOUTHERN
DUNLIN (CALIDRIS ALPINA SCHINZII) ON THE SOUTHERN BALTIC COAST
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Until the end of the last century, the dunlin was a common breeding bird along the southern Baltic coast. Because of the cultivation of the seashore meadows, its number has decreased very much. Now the dunlin breeds only in relatively few places.

In the GDR there are five breeding sites along the coast and one inland site. The largest breeding place is found in the middle coast - Darsser-Boddenkette, where about 45 pairs breed. In the country as a whole about 90 pairs breed.

In Poland, along the coast, about 80-100 dunlin pairs breed on three sites only. One with a single pair is far from the coast. The biggest breeding colony (about 60 pairs) is situated at the Gulf of Gdańsk near the mouth of the Reda.

In Lithuania and Latvia only single pairs breed on some sites along the coast and far from the coast. In Estonia the breeding population consists of at least 1000 pairs. Dunlins breed mainly along the coast there. The biggest concentration (about 30 pairs) is in the Matsalu reserve.

ÜBER DAS ZUSAMMENFALLEN DER MAUSER UND DER NESTPERIODE
BEI SPERLINGSVÖGELN (PASSERIFORMES)

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Es sind die Tatsachen des partielles Zusammenfallens des reproduktiven
Zyklus und der Anfangsstadien der Mauser wenigstens bei 45 Arten der Sper-
lingsvögeln, den Vertretern der folgenden 13 Familien bekannt: Hirundinidae
(2 Arten), Corvidae (3), Paridae (4), Pycnonotidae (5), Troglodytidae (1),
Turdidae (5), Sylviidae (7), Muscicapidae (3), Prunellidae (1), Motacillidae
(4), Sturnidae (2),Ploceidae (2), Fringillidae (6).

Diese Erscheinung wurde zuerst als Anpassung zur Fortpflanzung in hohen-
breiten (Blumental, Simin, 1966; Haukioja, 1971; Simin, Lapschin, 1974) und
im Hochgebirge (Kowschar, 1977, 1981) betrachtet. Diese Erscheinung ist aber,
wie es sich erwies, in der Waldzone von der Ostsee (Kukisch, 1974; Noskow,
1975) bis zum Sibirien (Moskwitin, 1972) und Fernen Osten (Neufeldt, 1971;
Netschajew, 1974, 1975); in den ariden Regionen von Australien (Keast, 1974)
und Afrika (Jones, 1978; Stutterheim, 1980) zu vermerken. Ähnliche Angaben
haben wir in dem Halbwüstenregionen im Norden des Kaspischen Meeres erhalten.

Nach der Analyse der Angaben stellte es sich heraus, daß das Zusammenfal-
len der Mauser und der Fortpflanzung weder von der Nestbauart noch von der
Nahrung abhängt. Die Ursache des Zusammenfallens dieser Vorgange ist, voraus-
sichtlich, in allen Fällen einzig und allein - die Knappheit des Zeitabsch-
nittes zwischen der Beendingung der letzten in dieser Jahreszeit Brut und dem
Anfang der Mauser. Das hängt nicht von den Faktoren ab, wodurch diese Knap-
pheit bedingt ist (polyzyklische Fortpflanzung; Spätbeginn der Fortpflanzung
bei der monozyklischen Art, klimatische Bedingungen der Gegend, Wetterbeson-
derheiten des entsprechenden Jahres usw.).

Die Erscheinung des Zusammenfallens der Mauser und der Fortpflanzung bei
den Passeriformen ist wahrscheinlich viel mehr verbreitet, als es heute
bekannt ist.


SOCIAL ORGANISATION AND ROLE OF HELPERS, IN ANTEATER
CHATS (MYRMECOCICHLA AETHIOPS) AND MOURNING WHEATEARS
(OENANTHE LUGENS SCHALOWI)

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Anteater Chats (AC) and Mourning Wheatears (MW) overlap in their distri-
bution and sometimes even share the same habitat. Both species have helpers
at the nest that aid in feeding the young during breeding. They are highly
territorial which may be due to the lack of suitable breeding sites. AC breed
in deep holes while MW breed in shallow holes or niches. In contrast to MW,
AC have no sexual dimorphism. This difference is reflected in the female's
behaviour. MW females sometimes go from one male's territory to others,
whereas AS have a lasting pairbond. Young AC stay with the parental group
until they obtain a chance to pair. Before leaving the group, males and fe-
males act as helpers. Female MW leave the parental territories soon after

fledging, while males remain longer and serve as helpers for later broods. At most, two helpers were observed feeding the young in MW.

Differences between the two systems, for example, group size, feeding rate of group members, breeding success and availability of suitable breeding sites, are discussed.

THE VARIATION OF THE KINGFISHER'S PREDATION DURING THE
REARING OF THE NESTLINGS (ALCEDO ATTIS L.)

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During our field studies on the kingfisher's ecology, we have found that this bird selected the size of his preys according to the age of the nestlings. During the first ten days of the rearing period, the adults catch small fishes ( $\approx 5$ cm). Larger preys are preferentially brought as soon as the nestlings are able to ingest them.

Sometimes we observed that in respect to the size selection, a strong variation existed in the relative abundance of the various species caught. Smaller species or age groups are caught at the beginning of the rearing period.

We also found variation in the feeding intensity. The food intake rate of the young rapidly reaches the level of about 9 fish per day but in the last five days before they fledge it falls to about 6 fish per day.

Our results show that the kingfisher's predation varies quantitatively and qualitatively in relation to the age of the nestlings.

THE EFFECT OF A PREY SPECIES, MICROTUS PENNSYLVANICUS,
ON NESTING, POLYGYNY, AND POPULATION DYNAMICS OF A
PREDATOR, CIRCUS CYANEUS HUDSONIUS

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On a 16.000 ha study area in Wisconsin the abundance of voles (Microtus pennsylvanicus) determined how many harriers (Circus cyaneus hudsonius) bred, at what age young males bred, and how many mates old males had. (These relationships were interrupted during a period of heavy aerial spraying with DDT.) The effect of the voles on the hawks may be physiological (in the intestinal flora of the voles?) or psychological (repeated stimulation of female being fed small prey?). Adequate quarry is available when voles are scarce, but tends to be larger. Birds that have reared young successfully tend to return to breed again. During vole highs especially, a "gypsy" cohort of harriers of unknown origin appears on the area. These two cohorts make up most of the breeding population. The possible role of polygyny in population regulation will be discussed.

This 23 year study is based on 275 nests, 541 nestlings banded and 208 color-marked breeding harriers.

MIXED SINGERS: THEIR RELEVANCE TO SONG LEARNING
AND SYSTEMATICS

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In bird species exhibiting a constant and species-specific song structure some individual males incorporate song features of alien species into their song or completely replace their own song by the alien one, respectively. These individuals are called "mixed singers".

Mixed singing appears to result from song tradition incidents, e.g. loss or lack of conspecific song models, rather than from genetic mutations of hybridization. When comparing all known and well documented cases for European songbirds, we found that in the major number of cases the imitated alien model is a member of a very close relative species (e.g. Certhia familiaris - C.brachydactyla; Acrocephalus scirpaceus - A. palustris; Phylloscopus trochilus - Ph.collybita). With regard to song learning, this could be explained by the selection of the model not only by acoustic but also by morphological or other criteria. In some other cases (e.g. Fringilla coelebs; Anthus trivialis), the spectrum of models is wider, these species not being close relatives but merely exhibiting similar song structure. This is interpreted by a selection mechanism of models which relays mainly on acoustic features.- Mixed singing generally is a rare event which does not seem to be specifically supported by selection. On the contrary, mixed singers have been demonstrated to reproduce successfully only in a small number of cases. Hence,mixed singing cannot be an effective way of competing with alien species.


SOUND PRESSURE LEVEL AND FREQUENCY SPECTRUM IN THE SONG
OF THE AQUATIC WARBLER (ACROCEPHALUS PALUDICOLA) IN
RELATION TO HABITAT ACOUSTICS

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The sound pressure level in the songs of several aquatic warblers was measured in the natural environment (Hortobágy, Hungary). The average sound pressure level of 100 syllables of one individual e.g. amounts to 63.5 dB (min 50, max 80 dB) at a distance of 2.5 m in an approximately free sound field. 1/3 octave analyses show that the "churring" syllables with a wide frequency spectrum have their maximum levels in 1/3 octave bands with filter centre frequencies of 4, 5 and 6.3 kHz (3.548-7.079 kHz) while more "melodious" syllables have them in 2.5 - and 3.15 kHz 1/3 octave bands (2.238-3.548 kHz).

Vegetation in the habitats of the aquatic warbler mainly consists of various kinds of grasses that can reach a maximum height of 1.50-1.80 m. The habitats differ from those of other Acrocephalus species in wanting of reed. The transmission of pure tones, random noise and played back songs of the aquatic warbler as well as of other species, typical and non-typical for the above described habitat, was measured in the natural environment with a loudspeaker - sound pressure level meter combination.

INVESTIGATIONS ON TERRITORIAL REQUIREMENTS OF THE
RINGED PLOVER (CHARADRIUS HIATICULA) AND THEIR
POPULATION-ECOLOGICAL CONSEQUENCES

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Territory size has been analyzed in relation to various intra- and extrapopular factors. The material was recorded for a colourringed population of avg. 34 (24-42) breeding pairs, which have been investigated for size determining mechanisms since 1974 as well as for 8 control areas with a total of 49 breeding pairs in 1980, all situated at the southern coast of the Baltic. Territory sizes have been ascertained by mapping of clutches being corrected by sample ethotopograms.

The territory is determined by the male and codominated by the female, serving for reproduction and for feeding which may also take place outside. Approx. 56% of territories are occupied by males faithful to their territory, 8% by males switching territories and 36% by newcomers.

The size of territories in 4 beach habitats was between 0.03 and 0.49 ha (avg. $0.28\pm0.11$ ha; n=183) and included a shore line of 0 to 193 m (avg. $86\pm46$ m; n=154). The corresponding size in two field habitats distant from the shore was avg. 3.49 ha (n=12).

Findings indicate negative dependences on settling pressure upon the individual area, on the structural resources of the habitat, and on the usable food supply. The social status is only important for the position of the territory, but not for its size. Efforts for maximizing territory size are not evident. Within the first days after hatching of the chicks, during which the family feeds almost exclusively within the territory, ownership of a shore-sector may be significant.

Territorial requirements have been evaluated as a component that determines the carrying capacity of a breeding area. They only limit the actual population size on small sites and short times. This does not exclude affecting population size in larger areas by spacing of individuals into suboptimal habitats and thereby reducing fertility.

INTERNATIONAL SURVEY OF ANTARCTIC SEABIRDS:
AUSTRALIA'S CONTRIBUTION

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At present, many nations are examining the possibility of commercial exploitation of Antarctic krill. This planktonic crustacean is the major food of several species of whales, seals, seabirds, fishes and squid in Antarctic waters. Informed management of krill as an exploitable resource requires knowledge of the stocks of krill and of their consumption by natural predators. Recognising the lack of relevant information for Antarctic seabirds, the Scientific Committee on Antarctic Research has implemented the International Survey of Antarctic Seabirds.

Penguins were selected for special study as they comprise about 80 per cent of the avian biomass in the Southern Ocean; most of these are Adelie

Penguins in the Antarctic, and Macaroni and Royal Penguins in sub-Antarctic regions.

Australia has undertaken to census breeding colonies of Adelie Penguins along the 6000 km coastline of the Australian Antarctic Territory, and Macaroni and Royal Penquins on Macquarie Island, Heard Island and the McDonald Islands. All existing population data have been compiled and detailed ground and aerial photographic surveys are underway. The paper will include results from the 1981/82 season, with new information on the food of Adelie Penguins.

THE FEEDING ECOLOGY OF AMERICAN FOREST VULTURES
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The 5 species of small American vultures (genus <u>Cathartes</u> <u>Coragyps</u> and <u>Sarcorhamphus</u>) have distributions centred in the neotropical rain forest region of central and South America. By comparison, none of the 15 species of vultures in the Old World are found in forests, and all species live in open habitats. The current study considers why several species of scavenging birds should have evolved in the tropical forests of the New World, while none have developed in forested regions of the Old World.

Studies on the food supply available for scavanging birds in forest regions suggest that this may be more abundant in neotropical forests than in African forests. Studies in Brazil and Panama on the exploitation of carrion on the forest floor indicate that the invertebrate community is important, and that and activity results in carcasses remaining available for scavenging birds for long periods of time. The foraging behaviour of forest vultures in being studied to determine their efficiency at locating carcasses.

PITCH AND RHYTHM MATCHING: AUDITORY FACILITATION
AND TRIGGERING EFFECTS OF ACOUSTIC STIMULI
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A prime concern of this paper is to add to the results on song type matching, further forms of vocal responsiveness which suggest a selective readout of auditory information on the part of the stimulated bird. In nightingales (<u>Luscinia megarhynchos B.</u>) pure tone series and rhythmically structured trill series are two characteristic song type features which are variable in terms of either pitch or temporal patterning. By playback experiments, it could be evidenced that both pitch and temporal patterning were responded to in a selective manner. Correspondence between syllable morphology (modulation, duration, etc.) did not prove to be an essential feature here. There are specific characteristics of pitch and rhythm matching which might point to different communicative functions.

BIRDS NESTING IN BUILDINGS OF TOWNS IN THE
LITHUANIAN SSR

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Over the last 10 years at least 16 species of birds nesting in buildings
were recorded in Lithuanian towns. Synanthropic species made the majority.
A number of species formed sedentary populations with changed behavioural
stereotype.

I. House martin (Delichon urbica), swallow (Hirundo rustica), swift
(Apus apus), feral pigeon (Columba livia), black redstart (Phoenicurus
ochrurus), house sparrow (Passer domesticus) nest only in buildings.

II. Jackdaw (Corvus monedula), starling (Sturnus vulgaris), spotted fly-
catcher (Muscicapa striata), white wagtail (Motacilla alba), great tit (Pa-
rus major), tree sparrow (Passer montanus), blackbird (Turdus merula),little
owl (Athene noctua) nest in urban green plantations and buildings.

III. Wheatear (Oenanthe oenanthe), tree creeper (Certhia familiaris) sel-
dom nest in buildings.


INTERPRETATION OF PHYLOGENY OF YELLOW WAGTAIL COMPLEX
(MOTACILLA FLAVA - M.LUTEA - M.FELDEGG)

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The original form of the yellow wagtail seems to have been very close to
the resident Egyptian form - Motacilla flava pygmara which had the most pri-
mitive plumage colour similar in both sexes. In their first winter plumage
the adult birds of this form are similar to the young of other forms.

The study in the alteration of the plumage colour and pattern of the head
in ontogenesis (admitting the archaic nature of female plumage) showed 4
ways of dispersal. (1) Middle-Palearctic - the development of yellow pig-
ment; (2) North-Eastern-Palearctic-the intensification of pigmentation;
(3) Central-Palearctic - depigmentation; (4) South-Eastern-Palearctic - the
development of black pigment. The last group seems to give two secondary
ways of dispersal - to the East and to the West. In the boundaries of each
way of dispersal the female plumage is progressing until the plumage of both
sexes becomes fully identical.


THE BLACKISH NIGHTJAR IN SURINAM

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The Blackish Nightjar Caprimulgus nigrescens is a small, sexually dimor-
phic, neotropical nightjar. Its distribution range is restricted to the Ama-
zon basin, including Surinam.It exhibits a wide ecological tolerance. The
habitat of this nightjar includes sandy savannas, open sites in second growth
and rain forest, and river banks. It is uncommon in more open savannas with
scattered bushes and more common on stony areas and rocky outcrops in forests
and on rocks and stony sand areas along rivers.

A population of this nightjar was studied on a large granite outcrop with scattered vegetation near Voltzberg in the Raleighfalls-Voltzberg nature reserve managed by the Foundation for Nature Preservation in Surinam (Stinasu). Roosting during daytime and foraging at night were investigated. Breeding behaviour was studied at several nests. The particular preference of the Blackish Nightjar for these granite outcrops in rainforests and the living conditions involved are discussed.

## ECOLOGY OF THE GOLDEN EAGLE (AQUILA CHRYSAETUS L.) IN NORTHERN BYELORUSSIA

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During 1972-1981 15 breeding territories (including 7 living nests) of the Golden Eagle were located over a 40000 km$^2$ study area in the northern part of Byelorussia rich in lakes and bogs. The total population of the Golden Eagle in this region is estimated 20 pairs. Common nesting habitats are big upland bogs exceeding 18-20 km$^2$. Nests are usually made on pines and aspens growing in forest isles and "noses" amidst the bogs. The minimum distance between neighborering pairs was 15 km.

Egg-laying begins approximately in the middle of March (13.3.1977). Nestlings hatch out at the end of April or at the beginning of May (7.5.1976 and 9.5.1979 chicks were about 7-8 days old). By the middle of June (15.6.1979) young were completely feathered. They left their nests in the second half of July (28.7.1979 a fledgling was seen near the nest).

On the average, a pair of Golden Eagles lays 2.0 eggs (by 3 clutches), brooks 1.8 nestlings (by 6 nests) and rears 1.1 fledglings (by 9 broods). Young Golden Eagles disperse in October. Among 444 food items predominated birds (67.2%) as well as hares (28.3%). In winter they regularly feed on carrion.

The only danger for the Golden Eagle is Man. In winter both young and old birds die in traps near animal carcasses and from poisoned baits.

As a result of drainage and cultivation of upland bogs the population of the Golden Eagle has considerably declined lately. In future breeding pairs might survive mainly in reserves where the principal elements of the landscape are bogs and woods.

## WEIGHT AND CHICK-MORTALITY IN THE BLACK-HEADED GULL (LARUS RIDIBUNDUS L.)

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Chick mortality was studied in 1974-1981 on the Lake Engure (Latvian SSR) using the method of fenced areas. Birds which reached their 25th day of life (a minimal age of flight) were considered as surviving.

Both the survival rate and average hatching-weight have the highest values in early clutches and then decrease during the season. The first and the

second chick in the clutch are the heaviest and survive best, the weight of
the third chick is about 7% less, its mortality is higher (both differences
are statistically significant). Differences in weight and mortality in 2-
chick nests are insignificant. Food plays the main role in chick survival.
In 1976 in one fenced area only one chick was left in each nest (indepen-
dently of the sequence of hatching) and their survival was significantly
($p < 0.001$) higher (91%) than in other areas (60%). The cause of lower sur-
vival of the third chick is not in its weight itself but in the lack of
food. In 1981 when either the first or the third chick was left in the nests,
their survival did not differ significantly (correspondingly 82 and 79%;
$p > 0.05$), although the difference in weight was 6.6%. Totally 63% of chicks
survived in this fenced area, survival in the neighbour control area and in
other areas with a normal number of chicks was significantly less - corres-
pondingly 38% ($p < 0.01$) and on the average 46% ($p < 0.05$).

INTERPRETATION AND SIGNIFICANCE OF TEMPORAL MIGRATION
PATTERNS AT AN ALPINE PASS IN COMPARISON TO STATIONS
IN THE LOWLANDS
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The autumn migration of Passerines in the area of influence of the Alps
is being investigated by a Swiss research program. Its aim is to describe
migration patterns according to sex, age and population, and, through com-
parisons with different ringing stations and radar studies, determine migra-
tory strategies is response to the Alpine barrier.

Capture statistics from an alpine pass (Col de Bretolet, VS) over a period
of 20 years are used to determine patterns of migration and differences with
lowland ringing stations. Particular emphasis is given to the analysis of
premigratory movements, the influence of the nearest breeding grounds, the
sources of the migrants, the site of the ringing station, the time of migrat-
ion, the distance of migration and the temporal distribution according to
age.

Once the significance of these factors have been determined, capture sta-
tistics can be used to determine migration strategies and may be used as de-
mographic indices.

COMPARATIVE BIOLOGY OF THE GIANT-PETRELS
MACRONECTES GIGANTEUS AND M.HALLI ON MACQUARIE ISLAND
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The giant-petrels Macronectes giganteus (Gmelin) and M.halli Mathews are
now widely accepted as a pair of sibling species. These largest members of
the family Procellariidae breed only on islands in Antarctic and sub-Antarctic
waters. They are sympatric at at least four locations near the Antarctic Con-
vergence, including Macquarie Island, but otherwise breed only either south
(giganteus) or north (halli) of the Convergence. Known attempts at hybridi-
zation have been unsuccessful.

Studies of their morphology, breeding biology and feeding ecology on Macquarie Island(sub-Antarctic), supplemented by information for giganteus from Antarctic stations and for halli from the Chatham Islands close to the Subtropical Convergence, suggest that giganteus is better adapted to Antarctic conditions and halli to those prevailing in the sub-Antarctic. Information on their dispersal from Macquarie Island, derived from distant recoveries of banded individuals, supports this view. The extent to which their eggs are contaminated with anthropogenic chamicals provides additional evidence.

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Populations of giganteus and halli that have been studied differ from those in the South Atlantic Zone north of the Antarctic Convergence. The giant-petrels breeding in this zone may be regarded as a third sibling species.


FURTHER OBSERVATIONS  ON THE POPULATION ANALYSIS OF BLACK
WOODPECKER INHABITING AN APPENNINIC REGION OF SOUTH ITALY
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World Wildlife Fund-Italy, Delegazione Campana, Riviera di
Chiaia 200, 80121 Napoli, Italy

This study presents some data on the ecology and distribution of Dryocopus martius in Campania, where this species is considered to represent   a relict of the last glaciation. This population in Campania, isolated from the rest of the Black Woodpecker population in South Italy, is probably bound to the progressive and continuous destruction of beech and spruce forests through the centuries. At the beginning of this century, the species was present in Central Appennino, and is at present found in the forests of Pollino and Sila. The Black Woodpecker was first observed in Campania about 25 years ago, mainly in summer months. Presently it is found through all major mountains of the area: Alburni, Picentini, Cervati, Gelbison, Maddalena.During winter months single individuals are seen, while in August they are seen in pairs. This information was also confirmed through hunters' activity. In one area shepards used to eat young individuals. Known stuffed specimens are 10 which have a 1:1 sex ratio. The habitat is composed mainly of vegetation with beech, white spruce and yews at 1100-1400 m above sea level, exposed mainly to the north and east. In 1975 a female bird was captured in the remnant of a mesophil forest,ca 20 km. from sea (70 m above sea level). Feeding and breeding habits were also studied. Ornithometric comparisons were made between this population and these from the Alps. In addition to this we have tried to study the ecological relationships of this species with other Picidae and man. We consider the presence of this species as the index of biolo-

gical and ecological integrity of the area and propose with strong conviction
that these areas be established as nature reserves.

PROBABILITY METHOD OF AGEING OF THE PASSERINE NESTLINGS AND
ITS USAGE IN THE INVESTIGATION OF THE BREEDING PHENOLOGY

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The method consists of the field determination of the nestling growth and
in the subsequent conversion of growth stages to age. The conversion tables
show the most probable age of the nestling's life and the probability of
this age being longer or shorter by one, two, etc. days. To show breeding
phenology, the probabilities of hatching on a given day in all nests should
be summed up, thus the obtained sums will form a distribution of probability
for the hatching period in the investigated population.

Determination of the growth stage is identical for different species but
conversion tables must be prepared separately for each. Growth is expressed
by wing length or the degree of feather development. Both these parameters
are strongly dependent on age and almost independent of food supply (there
are few exceptions, e.g. swallows), at least for the nestlings which are big-
gest among its siblings. The collection of both parameters in the field is
very easy. The method seems to be especially useful in gathering data on many
species by a number of researchers as is the case in collecting data for
nest record cards or for ringing nestlings.

ADAPTATIONS OF THE PASSERINE BIRDS FOR THE
LIFE IN KIRGHIZIA MOUNTAINS

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In the Tien-Shan mountains small passerine birds begin their breeding
earlier than in lowlands. The nesting density of the naturally lowland birds
is always below in mountains. Open-nesting Turdus merula and Lanius cristatus
have a higher nest-stand in middle mountains. The weight of house- and tree-
sparrows nest-stands flooring (feathers, hairs) increase with absolute height.
It is bound directly with low temperatures of the middle mountains. On the
other hand a weight of the vegetative materials of the nest is higher in low-
land nests of the same species. The statistical reliable difference of the
sizes, volumes and weight are considered in lowland and mountain eggs of
the Hirundo rustica and Passer domesticus. The smallspottiness of the egg's
colour increase in Hirundo rustica and Lanius cristatus with absolute height.
The tendency of decrease of the egg's number in the nests is considered in
mountains, the broods number is smaller here on the single pairs. The breed-
ing of the Passer domesticus and Passer montanus terminated almost simulta-
neously in the end of August on all altitudinal belts.

## DO NIGHT MIGRANTS USE THE SUN FOR ORIENTATION?

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European robins were held in closed rooms and exposed to a single light
spot beginning with sunset or after it the experimental birds were captured
migrants or birds helped for some time in visual isolation from stellar
cues. Analysis of orientation of experimental birds in round cages showed
that: (1) birds, raised under natural conditions, gradually shifted their
preferred direction in the oourse of the experimsnt. The azimuth of their
reaction to the stationary light cue corresponds to maintaining their mig-
ratory direction by the sun which is below the horizon at this time; (2)
young birds grown in isolation of stellar cues, or adults kept in isolation
sincs the breeding season maintained orientation without compensatory shifts
during the night in autumn experiments. The direction relative to the set-
ting sun remainsd constant almost the whole night. In morning hours birds
showed a drastic change in direction corresponding to one according to the
morning sun. These data allow us to propose that autumn migratory direction
according to the setting and rising sun is an inborn character, while com-
pensation ability to the visual sun shift is formed and corrected during
the course of the bird's life; (3) in all groups the directions according
to the light cue at sunset remain constant during the season. This fact sup-
ports the hypothesis of D.A.Vleugel, that direction of migration is selected
by night migrants on the basis of a constant angle to the setting sun.

## BIRDS' HEART RATE IN FLAPPING FLIGHT AND SOARING

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The paper deals with the analysis of the data presented by different
authors (Keskpaik, Horma, 1972, 1973; Berger, Hart, 1974; Kanwisher et al.,
1978; Butler, Woakes, 1980; Keskpaik, Leht, 1982) on the heart rate (HR) of
birds in flight obtained by telemetry.

For maximum HR values during flapping flight and lower values during soar-
ing and at rest, the allometric relationships "HR—body mass" were calculat-
ed and expressed as follows:

at rest (32 speciss).................... $HR_R = 20.3m^{-0.333}$ per sec,

in flapping flight (38 species)......... $HR_F = 27.4m^{-0.176}$ per sec,

in soaring (3) species ................. $HR_S = 182.0m^{-0.574}$ per ssc,

m – mass of a bird in grams.

The regression lines $HR_R$ and $HR_F$ have slopes, that when a body mass is
10 g, $HR_R$ is about twice as high as $HR_F$ and at body masses of 100 g, 1000 g
and 10000 g the former is about 3, 4 and 5-6 times higher respectively than
the latter.

The regression line $HR_S$ crosses both $HR_R$ and $HR_F$ in the points of body
masses of about 4000 g and 100 g respectively.

These calculations indicate that soaring is more economical in comparison
with flapping flight. Moreover, the larger the bird, the greater is the
effect.

ON REVEALING CAUSES AND TARGETS OF BIODAMAGING
EFFECT OF BIRDS IN THE INDUSTRIAL ZONES OF
SOUTH EAST EUROPEAN PART OF THE USSR

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As a result of observations made in the period of 1960 to 1982 and in various seasons 340 species of wild birds were registered in industrial zones of densely populated anthropogen landscape of the observed territory. About 10% of them are agents of biodamages of various objects.

Targets of their biodamaging effect are airplanes, powersupply devices, insulating, lacquer-colouring materials, plastics, glass, organic glass,wood.

New data about biodamages of technical devices and living objects by linnets, wagtails, tomtits are obtained.

The increased biodamaging effect of starlings and woodpeckers is registered at fish reception centres and fish breeding ponds, hunting industries.

Biodamages of insulators of the electric transmission lines caused by grey herons are also registered.

MAIN DIRECTIONS OF MIGRATIONS AND WINTERING PLACES
OF LARIDAE OF THE SOUTHERN WEST SIBERIA

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Based on the analysis of 150 recovered rings from the birds which had been ringed in 1966-1979 on the lakes of the Baraba and Kulunda steppes, general directions of the seasonal migrations and the places of wintering of the four species of Laridae have been ascertained.

Common Gull (Larus canus). In autumn, birds from southern Siberia fly off in different directions, but mainly inside the west-south sector. In October-November some part of Common Gulls mainly reach the places of wintering,those places covering the zone of the Azov Sea with the system of reservoirs in the Low Don and also the non-freezing coasts of the Caspian Sea and the inland reservoirs of Iran and Transcaucoausia. Some part of immature birds remain in the places mentioned above.

Great Black-headed Gull (Larus ichthyaetus). The main direction of the autumnal passage is south-western. While flying the birds keep close to the large fish basins of Kazakhstan (Naurzum lakes, the Aral Sea etc.). Wintering gulls ringed in Siberia were met near the coasts of the Caspian Sea and in northern Pakistan.

Herring Gull (Larus argentatus). The main direction of the autumnal migration is also south-western. At first some birds fly to the north, northwest or eastward, then they change their direction and turn to the southwest. Herring gulls winter in Mesopotamia (Dementiev, 1951) as well as at the south-eastern coast of the Caspian Sea and the southern part of Indostan. During the spring migrations the birds were seen in the region of the Amu-Darya middle stream.

Black-headed Gull (Larus ridibundus). The main routes of the autumnal migration are in the south-western sector. Some birds from the forest-steppe Western Siberia cross the Aral Sea and fly to the Iran coast of the Caspian

Sea and to Mesopotamia. The other part of birds pass eastward from the Aral Sea (between the Aral Sea and the Balkhash Sea) to the places of wintering, which are situated on the inland reservoirs in the south of Middle Asia, Afganistan and India. Thus, black-headed gulls nesting in the south of West Siberia winter on the spacious territory from Mesopotamia to the western coast of Indostan.

## NESTING BIRDS OF LENINGRAD

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A study of nesting birds of Leningrad was carried out in 1977-1981 in different biotopes of the city, namely in green plantations, in the regions with buildings erected in different years and in new districts not yet covered with buildings.

82 breeding species have been recorded, 21 are non-passerine species, 61 passerine ones. Of these 47 species are common, 24 are rare, and each of the remaining 11 species has been found once. Nesting of 6 additional species has been suggested.

The number of nesting species in families is as follows: Anatidae - 2; Accipitridae - 1; Falconidae - 2; Rallidae - 1; Charadriidae - 5; Laridae - - 4; Columbidae - 1; Strigidae - 2; Apodidae - 1; Picidae - 2; Alaudidae - 1; Hirundinidae - 3; Motacillidae - 4; Laniidae - 1; Turdidae -10; Sylviidae - - 12; Muscicapidae - 2; Paridae - 4; Sittidae - 1; Certhiidae - 1; Emberizidae - 4; Fringillidae - 9; Ploceidae - 2; Sturnidae - 1; Oriolidae - 1; Corvidae - 5.

Location of nesting species of birds within Leningrad is heterogenous. They are particularly abundant in old city parks and cemetaries-about 40 nesting species. 5-7 of them nest on the ground, about 10 nest in hollows and the rest nest in deciduous trees.

There are 5-6 species nesting in built-up areas of the city: Columba livia f. domestica, Apus apus (L.), Passer domesticus (L.), Corvus monedula L., Sturnus vulgaris L., Delichon urbica (L.), Motacilla alba L.

Representatives of meadow and field complexes (Charadriidae, Passeriformes) nest in sites not yet covered with buildings.

Colonies of Laridae nest near water. Some representatives of Anatidae and Charadriidae nest only in the south-western part of Leningrad located near sea.

No urbanized populations of Columba palumbus L., Turdus merula L. typical of western Europe inhabit the city.

## POTENTIAL FERTILITY OF WADERS IN TENGIZ-KURGALDZHINO DEPRESSION

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The investigations were carried out in 1969-1972 and 1977 in Reserve Kurgaldzhino. Nests with full clutches were taken into account to determine potential fertility. An average clutch-size of Haematopus ostralegus was 2.7 (2-4 eggs, n=3), Charadrius alexandrinus - 3.2 (3-4, n=6), Glareola nordman-

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ni - 3.5 (2-4, n=42), Chettusia gregaria - 3.6 (2-4, n=16), Charadrius du-
bius - 3.7 (3-4, n=19), Vanellus vanellus - 3.7 (2-4, n=79), Tringa totanus -
- 3.7 (3-4,n=64), Recurvirostra avosetta - 3.8 (2-5, n=78), Limosa limosa -
- 3.8 (3-4, n=37), Himantopus himantopus - 3.9 (3-5, n=59), Tringa stagnati-
lis - 4.0 (4, n=7). Two clutches of three eggs of V.vanellus, Ch.gregaria
and H.himantopus were apparently repeated after destruction of the previous
ones as they appeared in the end of May and in June. There were double lay-
ings of 6-8 eggs in some nests of H.himantopus and L.limosa. Infertile eggs
and eggs with dead embryos were: 1.7% of Ch.gregaria, 4.0% of R.avosetta,
6.8% of V.vanellus, 9.8% of L.limosa, 13.3% of T.stagnatilis, 13.5% of G.
nordmanni, 18.1% of T.totanus, 20.3% of H.himantopus. Addle eggs were not
recorded in the nests of Ch.alexandrinus and Ch.dubius. 131 (41.4%) nests of
316 observed were destroyed; they contained 430 eggs. The highest destructi-
on of clutches was recorded among Ch.alexandrinus (66.7%) and T.totanus
(48.5), the lowest among Ch.dubius (33.3) and G.nordmanni (34.1). The main
reasons were as follows: robbing by Corvus cornix, crushing by cattle, flood-
ing and desertion by parents.

### THE MOULT OF ADULT CALIDRIS MINUTA LEISL.
### IN THE TERRITORY OF KAZAKHSTAN

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No Calidris minuta Leisl. with moulting remeges or rectrices was known
within the Soviet Union (Kozlova, 1962). During 1969-1972 and 1975-1980, we
found that 15 adult individuals out of 5903 examined (in Central and South-
Eastern Kazakhstan) had renewed remeges or rectrices.

Complete postnuptial moult begins with the replacement of body feathers
in mid-July. Two specimens captured at Lake Sorbulak (Alma-Ata region) in
August, 23 and September 9 were in winter plumage with the exception of up-
per tail coverts. In July, quill feathers were moulted in 2 individuals(0.06%
of 3240 examined), in August - in 10 (0.4% of 2230), in September - in 3
(12.0% of 25). Nearly all of them were captured at Sorbulak Lake. Out of 12
Calidris minuta with moulted flight feathers, 7 individuals renewed primaries
only,one - primaries and secondaries and 4 - flight feathers and rectrices.
Three birds renewed rectrices only. The rectrix moult began about 13 July,
the primary feathers moult about 8 August, and the secondary feather moult
about 20 August. The maximal moult score (Snow,1970) was in specimens caught
on 23.August (21; 3 new and 2 growing feathers) and on 9 September (26; 4 new
and 2 growing). After this the last bird renewed secondaries (moult score 15)
and rectrices (moult score 8). It is likely that these birds continued the
moult during migration to winter quarters.

### ECOLOGY OF CAPERCAILLIE (TETRAO UROGALLUS L.)
### IN THURINGIA (GDR)

Siegfried Klaus
Jena, GDR

In the Thuringian area today about 100 capercaillies live in about 470 km$^2$
of woodlands in the Thuringian State Mountains and in the Saale-Elster Sands-

tone area (districts Gera and Suhl). The size of the area and the number of birds decreased within the last decade to about 40% as compared with 1970.

Causes of the decline have been changes in the habitat, increasing density of predators and the wild boar (Sus scrofa), and increasing recreation activities in the woodlands.

Most preferred habitats of capercaillie in Thuringia are secondary pine forests on poor soils with dense shrub layer of Vaccinium myrtillis and V. vitis-idea. Mosaic-like structures with high amount of border between different age classes of trees, natural rejuvination and small openings (including small clear cuts) were selected by the birds. Birds also prefer higher parts of the mountains (Tops, ridges, crests, southern slopes, plateau regions).

Despite generally mild climate conditions of the whole area, the reproduction success was found to be correlated positively with the mean temperature of June and negatively with the amount of rain fall. The density of birds and reproduction success was also negatively correlated with increasing density of predators and wild boar (as measured by the hunting bag within the last decade). For the protection of capercaillie in Thuringia the best habitats were selected and a system of reserves was established, which are subject to special habitat and hunting management (predator reduction).

## POSSIBILITY OF USING-HOLE-NESTING BIRDS AS BIOINDICATORS OF IMPACT EFFECT OF AIR POLLUTION ON FOREST ECOSYSTEMS

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Work took place in the zone of activity of Jonave nitrogen fertilizer plant in central Lithuania. Data compared with those collected in 1970-1980 from control plots. In Jonava district, air is polluted by $SO_2$ and $NO_x$ (mainly). In different distances from the plant, 400 nest-boxes were placed for small passerine birds. During 1979-1981 years, occupation of boxes, presence of different species, breeding success, quantity of second clutches in comparison with first, quantity of abnormal eggs and other parameters were taken. Considerable differences were found between clutch size, breeding success, between indices of form of eggs and egg measurements in different distances from the plant. Common Redstart bred in considerable density only in forest plots with high levels of pollution. Weight of eggs of Great Tit is lighter nearer the plant; comparative density of this species increases with greater distance from the plant. The density of the Pied Flycatcher increases closer to the plant.

## CONTRIBUTION TO THE KNOWLEDGE OF ANTROPIC INFLUENCE ON THE FORMATION OF ORNITHOCENOSES IN WESTERN TATRA (ZAPADNE TATRY)

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Incidence of ornithocenoses at the mountainous, supramountainous, subalpine and alpine level of the Western Tatras (Slovakia) is analyzed. Based on both the quantitative and qualitative evaluation it could be stated that all

values analyzed (quality, trophic, associations, quantity, biomass) were lower or low at the mountainous, subalpine and alpine level while being high at the supramountainous level. Human activities exert an influence in a decisive way mainly at the mountainous and in several areas of supramountainous level; they have interferred in the past as well as in the present into the nature of these sites. Although the supramountainous level bears some signs of human activities, old trees can still be found and there is a relatively rich bush level at the forest edges. Original natural conditions are found at the upper limit of the forest which is especially attractive to birds. A stepwise decrease in all values analyzed could be observed at the mountainous/subalpine border level. Climatic fluctuations together with a shorter vegetation period are decisive factors. Natural factors are decisive at the alpine level. In nesting species at the subalpine and alpine level, a highly concentrated dominance occurs which creats labile relations and a low level of homeostasis. The bird component of zoocenose in this extreme ecosystem is small, though belonging to the highest level of the trophic hierarchy with an important role as regulators of heterotrophic processes. Comparing present species composition of birds with that in 1870-1885 (according to the papers of A.Kocian), certain differences can be observed. Decline in number of avian species, both qualitative and quantitative values, is due to the interference of man on vegetation, and on water biotopes, to various human constructions, and to the year-around frequently enormous movement of people across the area under observation.

HATCHING REGIMES OF TUNDRA SHOREBIRDS AND FACTORS
DEFINING THEM

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Incubation regimes of 22 species of Shorebirds of Chukotka and Kolyma tundras were studied in 1972-1980. The hatching period of all these species has 3 distinct stages: egg laying, "hatching proper" - until nestlings begin release out of the eggshell, and the last period-incubation. Each stage is characterized by certain behavioural patterns of birds behaviour and certain regimes of clutch warming.

During the egg laying period Charadriiformes spend in nests daily from 2 to 55% of time. When the temperature falls the warming time increases; open nesting birds show more intensive clutch warming. With every next egg the warming period grows by 5 to 15%. Late and repeated clutches require 1.5 to 5 times more intense hatching.

At "hatching proper" stage different individuals and species of shorebirds spend daily from 83.9 to 98.8% of time on clutch warming. Apart from specific and individual pecularities the hatching density is affected by many other factors. Most important of them are: predation, weather conditions, and food supply. Hatching period of clutch with incomplete egg set is 5 to 12% less. The intensity of warming increases considerably during the first 2-3 days but later on remains relatively constant.

When incubation is coming to an end the total hatching period remains exactly the same as before, but there is a sharp increase in the frequency of short-term departures from the nest, and in the frequency of overturning the eggs. These changes are most evident in fair weather. The behavioural variables in the last incubation stage enable hatching birds to regulate, to a certain extent, the time of hatching proper.

## URBANIZATION IMPACT ON THE FAUNA AND BIRD-POPULATION OVER FOREST LANDSCAPES IN THE CENTRAL REGION OF THE USSR

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A comparison was drawn between the birds' nesting and winter fauna on the one hand and the bird population on the other over various kinds of landscapes; slightly altered ones, greatly altered landscapes of suburbs, and those of parks and urban living quarters. The degree of change in the landscape was indicated by the per cent of square meters of anthropogenically altered landscape, of population density and of the value of recreational load. The data were gathered in 1971-1980 in the Central region of the USSR European part by a universally - adapted methology for birds' count over established and random routes 7-13 km long, crossing the most typical sites of every area.

The more man-changed the landscape is, the less nesting species there are: over slightly changed wood areas - 54 species, over greatly altered landscapes - 35 species,over urbanized territories - 20 species while the density of birds population (on the average) increases: 376.6 - 591.7 - 669.8 couples per sq/km respectively. The same regularity holds true in winter period too. The more urbanized the landscape becomes, the fewer species there are: correspondingly there are 27-21-18, while the mean populations density increases: 210.2 - 687.7 - 1413.8 individuals per sq/km. Stenobiont dendrophyll species, stenophagus and those species that cannot bear any man-evoked disturbances appear in urbanized landscapes. The main body of city bird population is formed by ecologically plastic species - polyphages using food of anthropogenic origin. The composition and the density of bird population are less influenced by seasonal fluctuation in urbanized landscapes than in the slightly changed ones.

## NESTING OF THE BLACK VULTURE OF THE NURATAU RIDGE (UZBEKISTAN)

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Black vultures begin to nest in February. They mate in the nest two or three times a day. They actively guard their nest site, though they often settle in 150-200 m from each other and soare assembled by 2-3 pairs and more. Hatching is from late February up to early April. Most intensive hatching occurs in March. On the average clutches are 1.01 eggs (n=72). During incubation (54-56 days) eggs lose 10-12 per cent of their initial weight. Nestlings weigh 70-80 per cent of the initial egg weights. Fledging period

is 104-120 days, their weight at that moment is 7.2-8.8 kg. At this age the youngs still cannot take off a flat surface. At the beginning of October adults still feed the young in nests despite the ability of the young to fly over dozens of kilometers. At the end of October some vultures leave the area. On the 7th of November 1979 a young vulture was registered 1000 km southward' from the nest site. Breeding success on the average is 0.48 fledgings per pair or 0.52 fledgings per nest.There were 36-40 pairs of black vultures per 200 sq.km of Nuratinsky Reserve in 1980.

Number and breeding success of black vultures during 1978-1980 were relatively stable, howerver in 1981 due to weather conditions the number of clutches was reduced by 30 per cent.

BEHAVIORAL REGULATION OF NESTS DISTRIBUTION OF THE
COMMON EIDER (SOMATERIA MOLLISSIMA)

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The data were collected in the Veliky Island area (the Kandalaksha Bay of the White Sea). The feeding of the common eider on marine food restricts their nesting area to the coastal zone (within reach of the sea for ducklings). There are no special requirements for abiotic conditions, which potentially allows the species to nest evenly along all the coast rich in food, though the degrees of nest safety in various areas differ radically. In the areas available for terrestrial predators almost all the nests are practically destroyed, but in the areas unavailable for predators (99% of females nested) - only 30% of the nests are destroyed. The total square of the places, where the majority of destroyed nests were observed is much larger than that of the relatively safe ones, i.e. the birds are clearly capable of evaluating the safety of nesting. The played recordings of the males' breeding calls revealed that their recorded calls attracted the birds (particularly, the young specimens and male-bachelors) and stimulated their breeding activity. In spring the allocation of males over the area is determined by the distribution of females. But, because of great nest site fidelity (Wakeley, Mendall, 1976) the successfully breeding females concentrated near the previous year's nesting. Therefore, the intensity of sound background created by males was maximum in the area, where the greatest number of females nested successfully the previous year. As a result, the majority of the females nesting for the first time settle in the relatively safe places.

The positive response to the specific sound background of common eider females, which are not very attached to any concrete nesting places, gives a possibility to actively influence the nesting distribution of birds, to create optimal conditions for safety and the exploitation of the species.

TRANSKONTINENTALE VERBINDUNGEN VON DURCHZÜGLERN DES
NORD-WESTLICHEN SCHWARZMEER-GEBIETES

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In nord-westlichen Schwarzmeer-Gebiet sind 332 Arten von Brut-, Zug-, Invasionsvögeln und Wintergaste verzeichnet. 220 Arten dafon (das beträgt 66.26%

von der ganzen Avifauna des Gebiets) sind in der Zmeinji-Insel bemerkt worden. Während der Frühlingszeit werden hier 79 Arten täglich festgestellt. Nur in den letzten 4 Jahren waren in diesem Gebiet 3 für die Ukrainische fauna neue Arten gefangen, das sind Goldhähnchenlaubsänger (Phylloscopus proregulus), Fichtenammer (Emberiza leucocephalos) und Sylvia cantillans (die für die Fauna der UdSSR neue Art). Die Massenberingung (damit werde 1974 begonnen) erlaubte die Gesetzmässigkeiten der Migrationen, der jahreszeitlichen Verteilung und Winterungen für einzelne Arten zu ermitteln. Über 60000 Vögel sind beringt worden. Im nord-westlichen Schwarzmeer-Gebiet sind Vögel verzeichnet, die in folgenden Regionen beringt waren: Westsibirien, Unteres Wolga-Gebiet, Leningrader Gebiet, Ostsee-Gebiet, Finland, Norwegen, Schweden, BRD, Dänemark, Holland, Frankreich, England, Spanien, Mali, Nigerien, Senegal, Marokko, Südafrikanische Republik. Die im nord-westlichen Shcwarzmeer-Gebiet beringte Saatkrähen waren auf Winterquartieren in Bulgarien und Rumänien festgestellt; Kormoran – in Griechenland, Jugoslawien, Italien; Waldschnepfe in Griechenland; Säbelschnäbler – in Tunesien; Rotschenkel – im Nahen Osten; Brauner Sichler – in Mali, Senegal; Nachtreiher – in Tsad, auf Malta, in England, Spanien; Fischreiher – in Italien.

## COLONIALITY OF GREBES (PODICIPIDIFORMES) IN SOUTH-WEST SIBERIA AND ITS ADAPTIVE SIGNIFICANCE

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Coloniality of grebes in south-west Siberia is more or less pronounced. Strictly speaking only Podiceps caspicus is really colonial, under certain conditions – great P.cristatus and red-necked P.auritus. The size of the colony is 5-150 nests, the area they occupy is 0.1-3 ha. Most colonies (90%) settle in gulls' (Laridae) settlements. Grebes' nesting density reaches 150-1500 couples per ha. Loss of clutches – 40-100%. So far as the ultimate result is concerned, colonial and solitary nesting do not differ. Very extended period of reproduction is characteristic of both cases. Over small dense colonies reproduction is 70-90% syncronized. Grebes colonies are passive assemblages of birds, their structure depends on the character of nesting and to a less degree on the neighbourhood of gulls.

The adaptive nature of colonial nesting when compared to the solitary one is in the protection of their nests by gulls from birds of prey and also in better use of nesting basins and stations.

## OECOLOGY OF NESTING OF RED-BREASTED GOOSE (BRANTA RUFICOLLIS)

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In 1977-1980 studies of red-breasted geese nesting were carried out in the Taimyr Peninsula, and in particular, of the conditions for hatching and morphology of an egg with a view of cultivating the captive species.

The red-breasted goose begins its hatching from the first egg and the egg-laying period lasts 4-5 days. The hatching period lasts 26 days, the actual

hatching lasting 1.5 days. The temperature in the nest comes to 16.2°C at the low level, to 36.2°C in the middle and to 40.3°C at the point of the body contact with an egg. The temperature inside an egg is 37.5°C, the rate of temperature drop of an egg in the open nest is 5°C per half an hour. All in all 100 eggs were examined. The longitudinal diameter is 67.8±7.7; the latitudinal diameter is 44.3±2.4; formindex - 54.0±18.0; average index of displacement of the cross-section surface - 14.0; average index of difference of the polar zones - 9.9. With an average weight of an egg of 77.5 g its specific weight ranges from 1.075 to 1.077. The composition of an egg is: eggwhite - 52.6 percent, yolk - 37.5 percent and the eggshell - 9.9 percent. The height of the air chamber ranges from 3.5 to 4.2 mm. The thickness of the shell is 324 -- in obtuse end, 362 -- in equatorial part and 372 -- in the sharp end. Average number of pores - 1500 per 1 sq.cm, which more than three times exceeds the usual porosity for a goose egg.

POPULATION OF RED-BREASTED GOOSE (<u>BRANTA RUFICOLLIS</u>)
IN THE TAIMYR IN 1978-1979
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In 1978-1979 the authors estimated the population of the red-breasted goose in the Taimyr peninsula. The land estimations covered 1450 km while the aerial ones covered 5300 km, the total number of registered birds reached 6640. When making estimations, the data of land registrations of 1977 were taken into consideration (880 km with 1778 registered birds); the registration was carried out by V.F.Dorogov, V.A.Zyrianov, L.A.Kolpaschikov (1979).

Results have shown that about 75 percent of the total number of red-breasted geese make their nests and moult on rivers and only 25 percent - on lakes. Within the nesting area of 183 thousand sq. km, the total length of rivers suitable for red-breasted geese was estimated 7.000 km (700 sq.km) and the area of lakes - 650 sq. km.

Total frequences of cases when birds were found present (single, nesting birds and nestlings) varied from 30-43 to 15-25 individuals per 10 km on the rivers of the Western Taimyr; from 15-29.5 to 1.8-3 individuals per 10 km in the Central Taimyr; 3.5-6.5 to 1.8-3 individuals per 10 km in the Eastern Taimyr.

In the year of 1978 favourable for propagation, nesting birds made up 24 percent of the autumn population, single birds - 17 percent and the young ones - 59 percent. The total number of the red-breasted geese was estimated 19.3 thousand individuals. In 1979 which was a bad year for propagation,nesting birds made up only 12.7 percent, single ones - 55.1 percent and young birds - 32.2 percent, the total population being 17 thousand individuals.

BIRDS IN RESERVOIRS' ECOSYSTEMS
(BIOGEOCENOTIC AND ENVIRONMENTAL ASPECTS)

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Stability of reservoirs rests on a number of factors such as: the multitude variety of bird species, their enhanced numbers and enlarged value of their biomass, the naturally routine change of land and water sites in the twenty-four hours and with seasons, a wide variety of food components, a large-scaled and very speedy distribution of metabolism's products. Migrant and sedentary birds vary in so far as their participation in the production and consumption of substances is concerned, some birds use reservoirs and their littorals as breeding areas. During migration organic substances are withdrawn from the reservoirs more intensively and this weakens the evtrof
icational process.

Because of the decline in waterfowl and shorebirds populations' reservoirs are less exploited and the birds' role in the transformation of substances is weakened. The cycle of substances' transformation slows down and this makes the water eqosystems less productive. Thus the preservation of water eqosystem is secure when the number of water fowl and shorebirds is restored.


POPULATION STUDY OF DUNLIN (<u>CALIDRIS ALPINA SCHINZII</u>)
NEAR GDANSK, POLAND - PRELIMINARY RESULTS

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The study was started in 1979 in the estuary of the Reda River, northwest from Gdańsk. Over 60 breeding pairs of Dunlin were found on two isolated seashore meadows. It was estimated that on main study area (96 ha) 34 pairs bred in 1979 and 46 in 1980.

Dunlins arrive on the study area at the end of March and the beginning of April. The earliest pairs started egg-laying between 20th and 25th April, and before 10th of May 80% of pairs laid their first egg. New clutches can appear through the whole of May and even in the beginning of June; they are probably repeated nests. First chicks hatch about 20th of May. By the early July all birds leave the breeding area.

In 79-80, 70 nests were found; 30% of clutches were destroyed before hatching, most often by <u>Mustellidae</u> and crows. 81 chicks and 47 adult birds were ringed. Out of 19 adults ringed on nests in 1979, 4 were trapped again next year in a almost the same nest locality. The measurements of adults(wing and bill length ) are similar to those of Dunlins from Finnish Baltic coast.

STATUS OF THREE SPECIES OF EAGLES IN POLAND

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In 1980 an inquiry about the nesting places of White-tailed Sea Eagle, Osprey, and Golden Eagle was sent to foresters throughout Poland. Based on

the results of this inquiry and on information from years 1975-1980 given by
many ornithologists, numbers of Sea Eagle in Poland were estimated as 70-80,
Osprey - 30, and Golden Eagle - 10 occupied territories.

Previous estimation (1970) was following: Sea Eagle - 50, Osprey - 30,
Golden Eagle - 8-10 pairs. The increase in numbers of Sea Eagle is an effect
of better knowledge of these birds by foresters and greater activity of or-
nithologists rather than real increase, though in Barycz Valley (Silesia)
the numbers of breeding pairs increased as compare with 1970.

In 1980 breeding success of 25 pairs of Sea Eagle was 0.64 young per ter-
ritorial pair.

In 1981 the Committee for the Protection of Eagles was created to coor-
dinate the study.


NEW NESTING BIRDS OF THE ALTAI ALPINES

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In the last fifty years a number of bird species known to have habitats
in the plains at the foot of the Altai have been found nesting in the moun-
tainions part notwithstanding the severe climatic conditions. Botaurus stel-
laris started nesting on the lakes of Kanskaya steppe, on the Tenginskoye
lake and the lakes, situated in the Chuyariver valley. Previously Mergus mer-
ganser were not ever met on the Dgulu-Kule lake and the lakes of Tchulishman-
skoye plato with their marshy banks (Sushkin, 1938). Now during the nesting
period they are regular birds here. Moulting birds were also met here. Alcedo
atthis also appeared in the mountain part. Fulica atra started making their
nests on the lakes of the Central and South-East Altai the banks of which
are rich in near-water vegetation. Gallinula chloropus and Crex crex were met
in South-East Altai during their nesting period. Among the new nesting spe-
cies of South-East Altai there are Riparia riparia, Hirundo rustica and Re-
miz pendulinus. In the past years Coturnix coturnix have been found in the
mountainious tundra of Central and West Altai, along the river valleys and
in the larch light forests of South-East Altai. Streptopelia orientalis has
also appeared in Central Altai. Pyrrhocorax pyrrhocorax used to make their
nests in South-East Altai, in its rocks and clay precipices but in 1975-
1981 their nests were found in settlements, at the garrets of shepherd stand
buildings and behind the window platbands. Because of the changed landscape
(the felling of forests made it more steppelike) Alauda arvensis and Perdix pe-
rdix moved over and penetrated into the mountanious part. Change of habitat
and adaptation to mountainous conditions are prompted by abundant food avail-
ability and ecological flexibility of the species on the one hand and by an-
tropization of environment on the other.


THE DYNAMICS OF THE EIDER POPULATION IN THE EASTERN
PART OF THE BALTIC AREA IN THE LAST HUNDRED YEARS

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The first data on the nesting of eiders in Estonia go back to the year of
1873 (Russow, 1874). At present the nesting distribution of the Eider in the
1130

eastern part of the Baltic area is mainly limited to Estonia. In Latvia and Lithuania the Eider does not nest for lack of the main habitat - the marine islands.

The main tendencies in the dynamics of the number of eiders in this century: 1900-1913 the number of eiders increased in Estonia, Sweden and Denmark (Stoll, 1911; Olsson, 1951; Hilden, 1964), during World War I their number decreased rapidly, a new rise occured in 1920-1930 (Härms, 1928,1934), in 1935-1945 the number of eiders fell, epidemics, World War II (Kumari, 1954), from 1947-1950 on a new increase began and it's going on at present (Grenquist, 1965; Joensen, 1974; Onno, 1970; Kullapere, 1980).

According to the results of 1980 count more than 8 500 breeding pairs of Eiders were registered in Estonia, 65% of them were nesting at the Vilsandy and Matsalu State Nature Reserves. The Common Eider is the most numerous nesting diving duck in the eastern part of the Baltic area.

DISTRIBUTION OF SOME BIRD SPECIES AND THEIR
NESTS IN THE FOREST BIOCENOSIS

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To estimate the role of birds in a biocenosis, it is first necessary t determine the distribution patterns of each species and communities under study. Traditional bird census methods based on the preliminary subjective division of the territory at a number of stations and further comparison of the indices of the species abundance, diversity etc., yield rough relative results.

We studied the distribution correlation using the Krylov formula (Krylov, 1968). This method permits the following three conclusions: (1) there exists a correlation between a pair of distributions; (2) there is a negative association; and (3) the distributions are independent. To obtain the distribution, we generalized the results of mapping counts, i.e. each bird's occurrence and each nest during the breeding season in a sample plot (25 ha).The latter was divided into 100 squares (50 m x 50 m). The sample plot was located in the old coniferous forest of the southern part of Prioksko-Terrasny State Reserve (Moscow region). The distributions of pair of species occurrence points being compared, the correlation proved significant only between pied flycatcher (Muscicapa hypoleuca) and greater-spotted woodpecker (Dendrocopus major).

The comparison of 4-year-long nest distributions (1977-1980) between pairs of species revealed no correlation. A correlation was shown, however, between the nest distributions of tree and ground nesting birds. The comparison of the nest distributions of all species between pairs of years showed correlations between 5 pairs of the possible 6. This indicates a similarity of the nest disposition in the entire bird community from 1977 to 1980.

ECOLOGO–TAXONOMICAL OBSERVATIONS OF SPECIES
COMPOSITION OF HELMINTHS OF BIRDS IN GEORGIA

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The area of Georgia is very variable geomorphologically with a great diversity of climate, vegetation, soil and fauna. All of these determine the helminthfauna of game birds.

The results of our investigations show that water birds were infected mostly with nematodes (63%) of 92 species, next with trematodes (55%) of 66 species then cestodes (47%) of 60 species and last acanthocephales (19%) of 14 species. A total of 222 species of helminths were recorded in game birds.

The greatest percentage of infection was recorded for Anseriformes birds (95.4%) with 57 species of helminths,followed by Pelecaniformes(95.0% with 6 species of helmiths), Lariformes(93.9% with 7 species), Charadriiformes (93.8% with 24 species),Ciconiiformes(92.6% with 25 species),Colymbiformes (79.4% with 8 species), Ralliformes (78.5% with 5 species).

Analysis of the helminthfauna of the water birds of Georgia demonstrated the correlation with feeding, mode of life and systematic position of the host. Comparative study of the helminthfauna of systematically related species of water birds in Georgia and of systematically unrelated but ecologically similar species that the helminthfauna depended not only on the phylogeny of the host, but to an even greater degree on its mode of life, feeding and climatic factors, that is on the complex of ecological and environmental factors that influence the host.


DIE BIOTOPISCHE VERTELUNG DER BRUTWALDVÖGEL

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Es ist festgestellt, daß in flächenförmigen Flurgehölzen des Festlandes von Litauen mit einer Fläche bis zu 20 ha, dank der Mosaik der Biotopen, entstehen besonders günstige Bedingungen für das Leben mehrerer Vögelgruppen (es brüten 83 Arten mit durchschnittlicher Siedlungsdichte – 145.3±4.3 Paar pro 10 ha, Diversität nach Funktion von Shannon – 3.257). Die Siedlungsdichte der Vögel wächst nach dem Schema:Kiefer – Laub – Fichten – Gehölze, d.h. nach einem anderen Prinzip, als in Waldmassiven. Die Brutvögeldichte in flächenförmigen Gehölzen hängt von der Charakteristik der Baumartenanteile, der senkrechten Struktur der Gehölzstöcke, hydrologischem Regimes des Bodens u.ä. ab. Die Kronenbedeckung des unteren Stockes, die Fichten-menge im oberen Stock auch die Mosaik der ökologischen Bedingungen vergrößern die Siedlungsdichte der Brutvögel. Es ist ein Modell geschaffen, das die Dichte der Brutvögel in flächenförmigen Wäldern von kleiner Fläche beim Einfluß der Veränderungen der Komplexfaktoren der Umwelt characterisiert.

ADAPTIVE FEATURES IN THE WILLOW WARBLER'S ANNUAL
CYCLE (PHYLLOSCOPUS TROCHILUS) IN THE CONDITIONS OR
NORTH-WEST USSR TAIGA AREA

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The biology of the Willow Warbler was studied in 1968-1977 by trapping
and individual marking, examination of 18 thousand birds and 600 nests, by
recording the total number. The main adaptive biological features of the
Willow Warbler in the conditions of north-west USSR taiga are as follows:
partial coincidence of nesting with the postnuptial moult, overlapping of
post-juvenile moult with autumn migration, the increasing rate of post-em-
bryonal development and of post-juvenile change of plumage in young in-
dividuals from late broods, reduction of some behavioral reactions. In the
short period of favorable conditions all these features facilitate the syn-
chronization of individual cycles.


THE NUMBER OF WHITE STORKS IN THE USSR

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The number of the nesting pairs of white storks (Ciconia   ciconia cico-
nia L.) registered during the All-Union census of 1974 in the USSR was
49726. Compared with 1958, the number of white storks increased especially
in the Estonian SSR and in the RSFSR. The number of their nests registered
in 1958 in Estonia was 354 and in 1974 amounted to 1060. In 1974 in ten reg-
ions of the RSFSR were 3299 nesting pairs of recorded white storks. A remar-
kable growth of the number of these birds was noted in the Kaliningrad,Pskov
and Bryansk regions (three times as many and even more) and also in the Smo-
lensk, Kursk and Belgorod regions as compared with the respective data of
1958. It is noted that they have populated the new territories in the Nov-
gorod, Kalinin, Kaluga and Voronezh regions. The nesting areas of the white
stork in the USSR are spreading in the northeast and east directions.


MIGRATION OF BARNACLE GEESE THROUGH ESTONIA

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The Barnacle Goose population of the Barents Sea (Eastern Europe) mig-
rates on a rather narrow front. The width in Estonia is 100-150 km. The du-
ration of the migration in autumn is 8-37 days, on the average 23 days(n=12).
The  average period of the migration in spring is 40 days, the maximum is
72 days. Mostly the size of the migrating flocks of the Barnacle Geese is
51-100 ind. (31%) and 101-200 ind. (30%). The morning and evening maximums
and the midday minimums can be distinguished in the daily rhythm of the mig-
ration. Fair wind and the reduction of the air temperature in autumn trig-
gers the migration of Barnacle Geese. During migration wind and air tempe-
rature do not influence significantly the intensivness of the migration. Ac-
cording to the data obtained from aerial surveys up to 30 000 Barnacle Geese
stop in West-Estonia every spring.

TESTING THE SIGNIFICANCE OF INTERNAL CLOCK IN THE NIGHT
ORIENTATION OF THE ROBIN (<u>ERITHACUS RUBECULA L.</u>) UNDER
NATURAL SKY

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In closed cameras Robins displayed a time-compensated night orientation
in relation to a fixed point of light (Liepa, 1978; Katz, 1980). There is
no conformity of opinion on the functional basis of this reaction (see
Vilks at al., this issue). So since 1978 we have been studying the orientati-
onal behaviour of the Robin in a round netwall pen (diameter and height 5 m)
under the open sky. About 20 birds are let into the pen simultaneously and
their distribution under the ceiling of the pen is photographed in the cour-
se of the night by means of a flashlight. In autumn, irrespective of how
cloudy the sky is, of direction of wind, presence of azimuth of the moon,
the time of letting birds into the pen (before sunset or after the astrono-
mical darkness sets in), the Robin prefferred the direction corresponding
to that of its migration. Spring orientation, on the contrary, was to a con-
siderable extent affected by wind (positive anemotaxis).

The internal clock of birds was phase-shifted by +4, +4 and -3h in spring
and +6, -6 h in autumn. The experimental and control birds, supplied with
light reflectors for group separation on the photos, were let into the pen
simultaneously after astronomical darkness set in. The effect of vernal
phase-shifts is obscure at present. In autumn the experimental birds in
their first test under clear sky and a new moon showed a deviation from the
mean direction of controls, as could be expected in the case of time compen-
sated celestial orientation. These results are in agreement with author's
supposition that compensatory reactions of the Robin under the single light
clue reflects ability of this species to make use of the night celestial in-
formation on the basis of the internal clock.


SOME QUESTIONS OF OOLOGY

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The possibility of using the study of egg colour for systematization of
birds has protagonists (Kusiakin, 1954) as well as adverseriss (Lack, 1958).
D. Lack, taking the Turdine as an example has shown the dependence of shell
pigment on the character of nesting, more that on the degres of relationship
between different species. Accepting the conclusion of D. Lack, it is possib-
le, after the same example with the Turdine, to establish the "first-type"
of the egg colour and also of the nesting character of the whole group. Then
the degree of egg-pigment lightening can show the age of the transition in
different species from the open to the hole nesting. In cases of similar
types of nesting inside relatively narrow systematic groups of birds, the
egg colour can help to determine the degree of relationship between differ-
ent species.

So, the study of the egg colour can help classification, and to a great-
er degres comprehension of the development of separate species and groups.

THE <u>STERNA ALEUTICA</u> BAIRD POPULATIONS ON THE
TERRITORY OF THE USSR (RECENT SURVEY)

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The <u>Sterna aleutica Baird</u> is a rare species distributed sporadically
within a limited areal. It inhabits separate sites along the Far-East coasts
and lives in colonies. Not more than 100 pairs nest in the southern parts of
the Sakhalin (the Aniva bay, the Lebyazhye and Nevskoye lakes); about 700
pairs – on the north-east coast of the Island (Nabilj, Nyivo, Dagy, Chayvo,
Piljtun bays and others) and about 200 pairs – on the north-west coast (en-
virons of the Pogiby cape, the coast of Amur liman, the Baykal bay and
others). According to the records of 1976-1979, the total number of species
in the colonies observed on the Sakhalin amounted to about but not less than
1000 pairs. In 1972 the colony of 40 pairs (Leonovich, 1976) was observed
along the north-west coast on the Okhotsk Sea in the Tauyskaya bay near Ma-
gadan. Only four colonies consisting of 120 pairs were observed along the
west coast of the Kamchatka peninsula; however, this region was not given
proper attention and it's very likely that the nesting birds of this species
are much more common there. Seventeen colonies of 500 pairs have been recor-
ded on the east coast of the Kamohatka though some of the possible sites
have not been examined at all. According to the records of 1975-1979, the
total number of species in the colonies observed on the Kamchatka came to
more than 600 pairs and, the total of about 3000 pairs seem to inhabit Kam-
chatka. The site of the species in the south of the Koryak Highland (coast
of the Korf bay and the Apuka river mouth) was not established (Kistchinskiy,
1980). The total number of the <u>Sterna aleutica Baird</u> in the Soviet Far East
appears to come to approximately 4000 pairs.


THE STRUCTURE AND EVOLUTION OF AVIAN GENOME

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Comparative studies of avian DNA that have been carried out in the recent
years allow certain conclusions to be made about the principles of organizat-
ion of the genetio material in these vertebrates and its specificity compared
to other classes. Avian DNA has a characteristically low content of middle
repeated sequences that are represented in the genome by dozens to dozens of
thousands of copies; the number of unique sequences (individual genes and se-
quences with the number of copies up to ten) is on an average one and a half
times higher. The unique and repeated elements in the avian genome have an
organization of the type that has been previously described for insects only.
In this respect the birds drastically differ not only from fishes and mam-
mals but also from reptiles, the evolutionarily closest class. The content
of DNA per cell in birds is much lower than in other groups of vertebrates.

In the taxa of birds of different rank studied, the divergence of DNA se-
quences estimated by DNA/DNA hybridization, is comparable with that in other
classes of vertebrates, though it differs from it. The level of homologies in

the class of birds is similar to that of fishes and mammals. At the same time, hybridization of DNA of the species from one genus of birds has revealed a degree of divergence that is characteristic of the interpopulational and interracial differences between the species of fish and mammals.

The DNA/DNA hybridization technique is used for solving certain problems of taxonomy. It has helped to make some conclusions about the relatedness of Galliformes and Ratitae, of some species, genera and tribes in the family of Anatidae.

HYDROPHIL BIRDS IN THE TROPHIC CHAINS OF THE
AZOVO-BLACK SEA ESTUARIES
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Qualitative and quantitative dynamics of avian population is best displayed in the exchange of dominant groups (in summer fauna-Charadriiformes, in spring and autumn-winter-Anseriformes).

Trophic chains of ecosystems with participation of two types of birds: those locked in estuaries and mixed (locked in estuaries and agrocenosises). According to their trophic peculiarities all the hydrophil birds can be divided into three groups: (1) those feeding in estuaries mainly (feeding with macrophytes, ichthiophages, euryphagous); (2) those feeding in estuaries and agrocenosises (a wide spectrum of feeding, including water and earth organisms); (3) those feeding only in agrocenosises (a spectrum of feeding is represented only with earth forms).

Species and groups of species which are predominant in size and importance for the biological exchange of substances belong to the category of migrants, their total number is estimated to be 4.5 mln individuals. The role these migrants play in the trophic chains is determined by the duration of their stay in estuaries.

When the changes in the block of estuaries' producers are reversible the consumers of the first order become transit migrants. For the birds of other trophic groups, changes in the dynamics of their feeding behavior are observed.

In the ecosystems of the northern Azovo-Black Sea coast birds are the most labial part, and still it is the peculiarities of their trophic connections and of their position in trophic chains that define the qualitative nature of the avifauna.

A SCANNING ELECTRON MICROSCOPE STUDY OF PRIMARY
FEATHER BARBS
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A scanning electron microscope study of the barbs of primary feathers of the Golden Eagle Aquila chrysaetos and the White-tailed Eagle Haliaetus albiculla revealed the presence of a mat of micropapillae, approximately 1.5 m high, on the sides of the barbs below the barbules. Cell boundaries were clearly visible and small indentations in the barb surface suggested the sites of collapsed nuclei.

A gensral survey of primariss from specimens representing most Orders of birds showed that the micropapillae wers present in some members of the Ti-namiformes, Pelecaniformes, Ciconiiformes, Galliformes, Gruiformes, Capri-mulgiformes and Piciformes as wsll as in the Falconiformes. However, not all the members of a particular Order necessarily possessed the micropapillae. The survey also revealed some rather different surfacs fsatures, ths most complsx being the surface mat of rsticulated fibres notes on the primary barbs of the Curlew Numenius arquata and of ths Hsrring Gull Larus argen-tatus.

A study was also made in the Golden Eagle of feathers other than prima-ries which showed that micropapillae were present to a varying degree on the barbs of all the feathers examined.

Examples illustrating the different types of structure and the range of variation are given, and the taxonomic implications and possible functional roles are discussed.


MICRATION PATTERNS OF THE BLACK SWIFT

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Migration of black swifts was observed for 20 years (1960-1980) in the Courland Spit of the Baltic Sea. Regular summer migration side by side with spring and autumn one was established. As compared to the unstable character of spring and autumn migration, summer migration is characterized by fixed dates, established regular dates of black cwifts' crossing the flight's route and a large number of migrating individuals (from 6 to 35 thousand per day, from 20 to 75 thousand per season). Annually 92% of swifts en route cross the Courland Split in the period from June, 5 - to July, 20. The num-ber of summer migrants and their age groups seem to relatively correspond to the number of reproductive black swifts (the lower is the per cent of ef-fectively reproductive individuals, ths higher is the number of summer mig-rants, spscially in July). The black swifts moved in day time as well as in the night. High concentrations of flying black swifts during night feeding flights were established, most, numerous in the period of summer migration. Days of regular flight during summer migration were established. Blaok swifts oconcentrations in the night time seem to have a regional character and they ars always relatsd to large nesting colonies of the species.

The migration of black swifts might be seasonal - spring, summer and autumn, but also day and night onss which in their turn include regular mig-ratory and fseding flights.


FACTORS DETERMINING FORMATION AND STRUCTURE OF BIRD POPULATION OF THE ALPINE SON-KULE LAKE IN TIEN SHAN

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The Son-Rule Lake (3020 km above the sea-level) has very harsh natural climatic conditions. Its banks are mash-ridden with lagoon-type small lakes.

In the past 20-25 years noticeable changes in the population of nesting and migrant birds have occurred on it alongside with species endemic for Central Asia mountains such as <u>Anser indicus</u> and <u>Charadrius mongolus</u> and such common species as <u>Anas platyrhynchos</u>, <u>Anas strepera</u>, <u>Aythya ferina</u>, <u>A.fuligula</u>, <u>Tringa totanus</u> etc. lately <u>Cygnus cygnus</u>, <u>Anser anser</u>, <u>A.albifrons</u>, <u>Limosa limosa</u> etc. have started nesting here.

Originally the Son-Rule Lake did not have any fish. Fish started there in 1959 and it took root. As a result those previously very few and scarce nesting species became numerous and even predominant (Podiceps, Laridae, Sternidae, etc.); <u>Ardea cinerea</u>, <u>Phalacrocorax carbo</u>, <u>Larus argentatus</u> etc. started nesting there. On the whole the number of nesting species has gone up from 25 to 36 species. The <u>Anseriformes</u> prevail over nesting sites (13 species).

Of primary importance for forming the ornithocomplex of the Son-Rule Lake were: the flight route over this lake, available ecologic conditions including abundant food, no disturbance during nesting.

PECULIARITY OF THE HELMINTH FAUNA OF THE FLAMINGO
PHOENICOPTERUS ROSEUS PALL

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As a result of many years (1968-1977) ecological and parasitological investigations of the biocenosis in the extremely salty Lake of Tengiz (Central Kazakhstan) it was found that the flamingos nesting and molting there are greatly infected with cestodes, mainly with hymenolepidids. Invasion of the birds with other groups of helminths was inconsiderable.

Peculiarity of the flamingo helminth fauna (the prevalence of cestodes in it) is conditioned by the peculiar specific composition of the invertebrates inhabiting the lake Tengiz which are represented by Branchiopoda (<u>Artemia salina</u>, <u>Branchinella spinosa</u>) and Ostracoda (<u>Eucypris inflata</u>) mainly, since they are obligatory intermediate hosts of cestodes and the main feed-stuff of these birds.

The parasitological data received complement the information on feeding and seasonal migration of Central Kazakhstan population of flamingos.

FEEDING ECOLOGY AND BEHAVIOUR OF EUROPEAN WIGEON

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Plant digestion has been studied extensively in the domestic ruminants, but there has been little work done on the smaller herbivorous mammals and birds. The small body size of these animals accentuates the problem of obtaining sufficient energy from a food which is difficult to digest. Among birds the European wigeon <u>Anas penelope</u> is one of the smallest species which feeds on a plant leaf diet, and these problems are therefore particularly acute.

This study examines the behavioural and physiological strategies which this species employs to maximise its energy intake during the winter. Data will be presented on the behaviour of wild birds to demonstrate their site selection, food quality manipulation, the selection of food for quality and digestibility, and feeding time allocation. Studies on the physiology of digestion cover changes in the gut morphology with season, and changes in the digestive efficiency of birds with grass quality and height, using both wild and captive birds.

Preliminary results indicate that the birds are able to graze efficiently on relatively poor quality grassland, but that they demonstrate clear preferences for certain feeding sites and that these preferences are related to digestive efficiency.

## ON THE SIBERIAN WHITE CRANE IN CHINA
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The Siberian White Crane (Grus leucogeranus) is a migrant and winter bird in China. In the past, they were recorded as breeding around the margin of Dalainor Lake and Qiqihar of northeastern China (Lou et Lee, 1932; Meise, 1934; Cheng, 1976); according to Wilder and Hubbard (1938) they breed in Liactung in northeast China (reference to two eggs similar to those of the Common Crane, with larger markings, 95 x 63 mm). However the reliable brreding records of this crane have not been registered in recent years.

In late May and early June 1981 a flock of 24 white cranes we saw in Wuyur river near Qiqihar of Heilongjiang Province; they were all subadults. and we considered them as migrants at the stopover.

During the spring and autumn migrations, they migrate along the Nen-jiang River in central parts of Heilongjiang Province and also southward along the coastal province to their wintering grounds. In spring 1945 a migrating flock of about 600-700 and in autumns (1943-1945) 357 White cranes were seen by Hemmingsen at the Beidaihe Beach, Hebei Province (Hemmingsen, Guildal, 1968).

The wintering grounds of White crane in China are known at the Lower Yangtze River (Cheng, 1976). In January 1981 a wintering flock of more than 100 White cranes were found at the west shore marshes of Poyang Lake in northwest Jiangxi Province (Chou et al., 1981). In addition a wintering flock of White cranes was seen by Wang (1981) in the Anqing district of Anhui Province.

## THE DISTRIBUTION OF BLACK-NECKED CRANE IN CHINA
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The Black-necked Crane (Grus nigricollis) is a world's only alpine crane species, its nesting areas are between 3500 to 5000 m above sea level, and even in winter it is the exception for cranes to migrate to warm lowland areas.

The Black-necked crane has been known to breed in the Qinghai Provence, northwestern Sichuan Province and southern Xizang Autonomous Region, and also

has been seen in the vicinity of upper reaches of the Indus River in south-western Xizang (Lavkumar, 1955). Stresemann et al. (1938) have reported its breeding at nothwestern Kansu Province, but not in recent years. The density of breeding population is 1.45 cranes per $km^2$ (mid-April to mid-May) and 0.76-078 cranes per $km^2$ (June) in 45.0 $km^2$ of breeding area at Lonbaotan (4200 m altitude), southern Qinghai Province according to preliminary surveys in 1978-1979 by Lu et al. (1980).

During the fall migration it has been seen sometimes in large flocks. Cheng wrote (1981) that a migrating flock of about 300-400 cranes was seen in September 1973 at the Tangra Range pass (about 5000 m altitude) flying southward; and in mid-October 1979 a flock of at least 600 cranes was seen in Nuomuhong in the Tsaidam Basin.

The cranes spend the winter is southwestern Sichuan, southern Xizang, western Guizhou and Yunnan. In early December 1979 a wintering flock of 70-80 cranes was found at the Caohai (grass sea, 26°51'N; 104°14'E; El.2200 m) in Weining of western Guizhou Province, they shared roosting together with Grus grus lilfordi (Chou et al., 1980).


CAPTIVE CRANES IN NORTHEASTERN CHINA

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A number of 7 species of cranes are kept in zoos or parks of Northeastern China. According to a rough estimate the species and numbers of captive cranes in 1980 are presented in Table 1.

| Cranes | a number of zoos or parks | number | | | | Total |
|---|---|---|---|---|---|---|
| | | male | female | sex uni-dentified | juve-nile | |
| Grus japonensis | 18 | 49 | 38 | 5 | 6 | 98 |
| Grus grus | 13 | 50 | 28 | 10 | - | 88 |
| Grus vipio | 8 | 17 | 10 | - | 6 | 33 |
| Grus monacha | 3 | 3 | 2 | 3 | - | 8 |
| Grus leucogeranus | 2 | - | - | 2 | - | 2 |
| Anthropoides virgo | 11 | 15 | 9 | 12 | 1 | 37 |
| Balearica pavonina | 1 | 2 | 2 | - | - | 4 |


ADAPTIVE FEATURES OF COLONIAL NESTING UNDER FLUCTUATING ENVIRONMENTAL CONDITIONS

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The study was carried out in the delta of the Selenga River (Southern Baikal) (1973-1980) on 8 species of Gull birds: herring gull, common gull, black-headed gull, little gulls, common tern, white-winged black tern, whiskered tern and caspian terns. The peculiarity of the Selenga River is the mountain-floodlands character of the water regime, resulting in fluctuations of water level by seasons as well as by years. At the beginning of the season the location of

colonies depends on water level which is stable by that time and by the peculiarities in the distribution of food resources. Since the fluctuations in the water level lead to qualitative changes of the inshore biocenoses, the location of colonies changes not only annually but what is more essential all throughout the breeding season. Since the value of fluctuations is relative, the search for optimal nesting sites is made by the "trial and error" method. The birds nest in small colonies of 50-80 nests, with high degree of synchronized breeding, occupying the maximum number of habitats. With the changes of hydrological regime and with the loss of colonies the birds nest again once moving up to the survival habitates and forming complex colonies of 150-200 or 1000 and more pairs.

Nesting by small colonies makes the birds very sensitive to any changes in the conditions of the habitat and promotes most rapid occupation of best favourable sites. Synchronized breeding in the colony helps to make use of most favourable conditions in the shortest time possible.

BIRDS ADAPTATION TO CONDITIONS OF RESERVOIRS ON
THE DNEPER RIVER

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Filling - in of reservoirs·causes a concentration of birds mainly waterfowl in the shallow islandic zone. New species nest there. Bird concentration leads to their increased activity as well as to antagonistic behaviour in the habitats of high nesting density.

Territorial fidelity is very marked and is accompanied by ecological plastisity, i.e. change of nesting habits and use of unusual sites for nests. The latter is temporary though it is extremely frequent.

During the formation of the reservoir the density of islandic birds population is decreasing while the duration of the breeding period because of unstable hydrological regime is considerable. At the same time birds tend to concentrate on separate islands and the number of colonies goes down.

Molting birds concentrate on reservoirs. A number of migrants and the duration of their stay on new reservoirs is essentially increasing. Frostproof parts of reservoirs near dams are favourable sites for wintering of some waterfowl.

THE ENERGY REQUIREMENTS AND ROUTES OF HEAT LOSS OF
INCUBATING GREAT TITS

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Recent investigations of the amount of heat lost by Great Tits during incubation showed that the heat loss increases considerably during the transition phase from egg-laying to incubation.

There are indications that the female will not start incubation when low temperatures would force her to exceed a certain level of heat production, but those cold spells after the onset of incubation do not bring about an interruption of the incubation.

An analysis of the changes in the heat loss pattern during the egg-laying and incubation period will be presented and discussed.

ADAPTATION OF BIRDS TO THE CONDITIONS OF
RESERVOIRS OF SOUTHERN UKRAINE
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The following types of adaptation of birds to the conditions of reservoirs are established:

1. Biotopic. This occurred due to abrupt changes in land ecosystems in the areas of reservoirs. This type of adaptation is manifest in the change of sites ,and breeding stations. Many typical crowners come to nest in bush, in tree stubs, in old demolished buildings (Milvus korschun, Buteo buteo, Corvus corax). Species, which previously nested on glasslands, sand banks, spits moved to placor conditions.

2. Phenologic. This arose from changes in the characteristics of ice dirfting and from readily evailable feeding objects. Many typical migratory birds became permanent residents (Anas platyrhynchos, Anas strepera, Anas querguedula, Larus ridibundus, Sturnus vulgaris). Migrant species (Aythya ferina, Anas penelope, Colymbus cristatus, Aythya marila, Oidemia fusca)came to winter; Larus argentatus, Colymbus nigricollis, Philomachus pugnax have begun to nest in the area.

3. Migrational. This is manifest mostly in the change of time and intensity of transmigration. Earlier the transmigration of northern populations of birds was simultaneous with the departure of local populations. The stop of northern migrants was short (up to 3 to 5 days). After the formation of reservoirs a gap was formed between the departure of local populations and the arrival of northern ones. The transmigration of northern populations became more prolonged and shifted 20 to 40 days later.

4. Reproductive. This is manifest in change of birds' fecundity. Average number of eggs in a clutch of reed and bush birds is 6.3 to 8.1 percent smaller. On the contrary, land birds in water biotopes, crowners and hole-nesting birds have larger clutches (increased by 15.2, 6.4 and 3.2 percent respectively).

TRAPPING AND MEASURING MIGRANT BIRDS IN LOMBARDY, ITALY
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Passerine birds have long been trapped in Lombardy during the autumn.The proper standardization of this activity is now needed since it might allow the collection of vast amount of new information. To this end, we measured body weight, total length, wing, tail and tarsus lenghts in several thousand specimens of some common passerine birds trapped in Lombardy from August 25th to December 10th. The data have been submitted to statistical analyses and simple correlations between parameters have been calculated.

Due to the large number of birds trapped, this approach seems promising to collect basic data for population studies.

## SOARING BIRDS' MIGRATIONS IN BULGARIAN BLACK
## SEA COSTAL AREA

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In this paper the results of visual observations of soaring birds' migrat-
ions during three consecutive years in the period from 10th to 30th of Octo-
ber is given. In the Autumn of 1981 the results of the visual observations
were supplemented with radar met's data. The information about quantity,
dates of passings, top migration days, spending of nights and ways of pass-
ing above the Bulgarian Black Sea costal area was collected on each to the
observed species.

The dependance between the migrating species' quantity and meteorological
conditions (direction and power of wind, atmosphere pressure, cloudness, fall
of precipitations, air temperature etc.) was assertained with the help of
e.c.m.

The results of this are of fundamental scientific, nature preservational
and practical importance.

## SELF-REGULATION OF NUMBERS IN BREEDING DUCKS
## AND ITS PROBABLE RELATIONSHIP WITH CARRYING
## CAPACITY OF NESTING HABITATS

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Recent banding results of the Tufted Duck have been summarised according
to a special program from 1961 on the Engure Marsh (Latvia). Relationship has
been observed among the yearly fluctuation in numbers of nesting females,
yearly changes in carrying capacity of nesting habitats and self-regulation
in female numbers. The basic indirect proofs on the role of fluctuations in
carrying capacity of nesting habitats in the dynamics of number are analyz-
ed: (1) lack of synchronity in yearly fluctuations of number of nesting fe-
males in various areas, and (2) correspondingly, a considerable autonomity
of self-regulation of numbers in these areas. More definite are the variat-
ions in survival of juveniles with the change in numbers of nesting females
compared with their number in the previous year. In years of various rate of
increase of nest numbers, a gradual rise in survival of juveniles correlated
to slowing in the increase rate has been observed; it usually continues to
rise after a slight decrease in nest numbers. Maximum is reached at 80-90%
which is close to the mean per cent of returned adult female-residents (65-
80%). At further drop in nest numbers, survival of juveniles also falls
sharply supposedly due to sharp competition among the residents for nesting
sites. The similarity of survival curves under various conditions allows the
suggestion that even little noticed variations in environment lowered car-
rying capacity of nesting habitats is often the reason for drop in nest num-
bers. Within the limits of usual fluctuations in number of breeding females,
the mechanisms of quantitative self-regulation practically eliminate the pos-
sible negative consequences of yearly fluctuations in carrying oapacity.

METERNAL ALARM CALLS OF MALLARD DUCKS (<u>ANAS</u>
<u>PLATYRHYNCHOS</u>): PRODUCTION AND ·PERCEPTION

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While brooding their young on the nest, female mallards occasionally
adopt a seemingly wary and elert posture (i.e., neck outstretched and head
held high) and utter low-amplitude alarm calls. These calls, which are ut-
tered when there is some disturbance in the vicinity of the nest (i.e., po-
tential predators), have an inhibiting effect on duckling vocal and locomo-
tor activity (i.e., "freezing" and cessation of vocalizations). This effect
occurs both in the field and in the laboratory, the latter involving mater-
nally-naive (i.e., incubator-hatched), one-day-old wild and domestic (Pe-
king) mallard ducklings.

This poster describes the specific acoustic features of maternal alarm
calls that effect behavioral inhibition in ducklings.

References: Miller, D.B. (1980) J. comp. physiol. Psychol. 94: 606-623.
Miller, D.B. and Gottlieb, G. (1978) Anim. Behav. 26: 1178-1194. Miller,
D.B. and Gottlieb, G. (1981) J. comp. physiol. Psychol. 95: 205-219.

HERRING GULLS POPULATION IN CAMPANIA DURING THE
LAST 20 YEARS

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There is little information on the gulls (<u>Laridae</u>) from southern Italy;
the present data are the first of their kind on herring gulls from Campania.
These are observations on nesting sites, on population size and on social
behaviour. We have noted a decline in the nesting sites found mainly along
the rocky surface of calcareous origin of the islands and on the rocks in
the Gulfs of Naples and Salerno. Today the herring gulls tend to abandon
the coastal sites and prefer to breed on the islands, concentrating their
colonies along the rocky surface of Capri Island. Capri, today, is practical-
ly at the center of the distribution area of this species in Campania. A
decline of nesting sites or total lack of them occurs in areas with major
tourist activity (specially in 1967-1971).

An increase in the number of nesting sites was found in areas of high
fish density and with a high density of shipping lanes. The colonies are
mainly oriented toward south and southwest. An analysis of size of these po-
pulation indicates that they consist of aging individuals, since there is a
considerable decrease in the number of immature individuals as a percentage
of mature individuals; there is no consistent decrease in the total populat-
ion.

It may be due to decreased reproductive activity. The immature indivi-
duals use different roosts for sleeping and for fishing. They prefer mainly

anchovies, herrings, mullets and Lamellibranchi.

There is high competition in winter with the migratory Blackheaded Gulls.

## TOWARDS A NEW CLASSIFICATION OF BIRDS

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During the last 50 years of stagnation in the development of avian classification, new data has been acquired making a rearrangement of avian families possible, because the orders in the Fürbringer-Gadow-Wetmore tradition are more ecological than systematic groups. The most valuable contributions have been studies on egg-white proteins (Sibley, Ahlquist), columella morphology (Feduccia), brain morphology (Mlíkovský), and numerous paleontological studies (Olson, Feduccia and many others).

A large amount of data gathered were evaluated by means of new methods of biological systematics (developed by Mlíkovský) which have been based especially on new achievements in mathematical logics.

The classification presented here is by no means definite: it will rather stimulate new ornithosystematical research. The following categories are used: classis, subclassis (-ida), ordo (-formes), subordo (-formia), and familia (-idae). The families refer, if possible, to those of Wetmore (1960). The orders within the Archaeopterygida and Hesper-ornithida are artificial.

Aves:

Archaeopterygida (for the Jurassic radiation):

Archaeopterygiformes: Archaeopterygidae, Preornithidae

Hesperornithida (new subclass for the Cretaceous radiation; type: Hesperornis Marsh 1872):

Hesperornithiformes: Hesperornithidae, Baptornithidae, Enaliornithidae (incl. Pelagornithidae), Elopterygidae, Cimolopterygidae (incl. ?Laornithidae, ?Torotigidae), Ichthyornithidae (incl. Apatornithidae, Angelinornithidae)

Telmatornithiformes (new ordo; type: Telmatornis Marsh 1870): Telmatornithidae, Palaeotringidae

Alexornithiformes: Alexornithidae

Struthioniformes: Struthionidae (incl. ?Eleutherornithidae), Aepyornithidae, Rheidae (incl. Opisthodactylidae), Casuariidae (incl. Dromiceidae, Dromornithidae)

Passerida (new subclass for the 1st branch of the Cenozoic radiation; type: Passer Linné 1758):

Alciformes: Prophaethontidae, Stercorariidae, Rynchopidae, Alcidae, Anoidae

Ardeiformes: Phaethontiformia: Gaviidae, Phaethontidae; Ardeiformia: Ardeidae (incl. Cochleariidae), Sulidae, Phalacrocoracidae, Plotopteridae, Anhingidae, Opisthocomidae (incl. ?Onychopterygidae)

Bucerotiformes: Bucerotiformia: Upupidae, Phoeniculidae, Bucerotidae; Eurylaimiformia: Eurylaimidae, Philepittidae

Ralliformes: Rallidae (incl. Orthocnemidae, Aramidae, Psophiidae, Indiornithidae), Gallinulidae, Heliornithidae, Rhynochetidae, Eurypygidae, Mesitornithidae, Turnicidae (incl. Pedionomidae), ?Raphidae, Cariamidae (incl. Phororhacidae, Psilopteridae, Brontornithidae, Cunampaiidae, Hermosiornithidae), Bathornithidae (incl. Geranoididae), Gastornithidae (incl. Diatrymidae, Dasornithidae).

Accipitriformes: Cuculiformia: Cuculidae, Centropodidae; Accipitriformia: Accipitridae (incl. Pandionidae), Sagittariidae; Phasianiformia: Phasianidae (incl. Tetraonidae, Numididae, Meleagrididae, Rhegminornithidae), Cracidae (incl. Gallinuloididae), Megapodiidae

Strigiformes: Strigiformia: Strigidae (incl. Tytonidae, Protostrigidae), Leptosomatidae, Steatornithidae; Caprimulgiformia: Archaeotrogonidae,Caprimulgidae (incl. Nyctibiidae), Podargidae Oincl. Aegothelidae), Musophagidae (incl. Couidae, Apopempsidae); Falconiformia: Falconidae

Columbiformes: Meropiformia: Halcyonidae, Todidae, Momotidae, Meropidae, Trogonidae; Columbiformia: Columbidae

Trochiliformes: Coraciiformia: Primobucconidae, Bucconidae, Galbulidae, Coraciidae (incl. Brachypteraciidae); Trochiliformia: Apodidae, Trochilidae

Tyranniformes: Tyranniformia: Tyrannidae (incl. Oxynuncidae), Querulidae (incl. Phytotomidae), Pipridae; Furnariiformia: Thamnophilidae (incl. Conopophagidae), Scytalopodidae, Furnariidae, Dendrocolaptidae

Passeriformes: many families with less known relationships

Ciconiida: (new subclass for the 2nd branch of the Cenozoic radiation; type: Ciconia Brisson 1760):

Apterygiformes: Procellariiformia: Procellariidae (incl.Diomedeidae, Hydrobatidae, Pelecanoididae), Spheniscidae; Apterygiformia: Dinornithidae (incl. Anomalopterygidae), Apterygidae; Tinamiformia: Tinamidae; Podicipediformia: Podicipedidae; Dromadiformia: Dromadidae; Chioniformia: Chionididae

Ciconiiformes: Ciconiiformia: Ciconiidae (incl. Balaenicipitidae), Pelecanidae (incl. ?Cyphornithidae), Fregatidae, Scopidae; Odontopterygiformia: Odontopterygidae (incl. Pssudodontornithidae); Vulturiformia: Vulturidae (incl. Neocathartidae, Teratornithidae); Charadriiformia: Charadriidae, Glareolidae, Pterocletidae, Laridae

Anseriformes: Phoenicopteriformia: Presbyornithidae (incl. Telmabatidae), Phoenicopteridae (incl. ?Agnopteridae, ?Scaniornithidae, Palaeolodidae), Recurvirostridae, Haematopodidae, Burhinidae; Anseriformia: Anseridae (incl. Paranyrocidae), Anhimidae; Otidiformia: Otididae (incl. Gryzajidae); Jacaniformia: Jacanidae, Rostratulidae; Gruiformia: Gruidae (incl. Eogruidae, Ergilornithidae)

Plataleiformes: Plataleidae, Scolopacidae (incl. Phalaropodidae)

Piciformes: Pteroglossidae, Capitornidae, Indicatoridae, Picidae

Aves inc. sedis: Aegialornithidae (incl. Hemiprocnidae), Cladornithidae, Dakatornithidae, Halcyornithidae, Marinavidae, Primoscenidae, Thinocoridae, Zygodactylidae

Passerida inc. sedis: Acanthisittidae, Pittidae

Ciconiida inc. sedis: Coliidae, Psittacidae

not avian: Bradycnemidae, Caenagnathidae, Gobipterygidae.


ENCEPHALIZATION OF BIRDS

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The study of the brain weight (E) to body weight (S) relationship in different taxa is a basic prerequisite to the investigation of brain size evolution.

In this study encephalization of 409 non-passeriform and 9 passeriform species was estimated by measuring volume of their cavita cranii. Additional data on 139 non-passeriform and 107 passeriform species were compiled from literature resulting in a knowledge of encephalization of 438 (=11.6%) non-passeriform and 109 (=2.7%) passeriform species. For each species, brain size of 1-127 individuals has been measured.

The results are presented in the form of allometric equations; correlation was tested with Kendall's tau. All correlations are significant at $p = 0.01$.

Aves:
$$\log E = \log 0.1528 + 0.5389 \pm 0.0414 \log S$$
$$\text{tau} = 0.6947, \ n = 547$$

Non-Passeriformes:
$$\log E = \log 0.1529 + 0.5369 \pm 0.0453 \log S$$
$$\text{tau} = 0.7059, \ n = 438$$

Passeriformes:
$$\log E = \log 0.0865 + 0.7257 \pm 0.0066 \log S$$
$$\text{tau} = 0.9086, \ n = 109$$

MORTALITY OF BIRDS ON THE ROADS AND THEIR DENSITY
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It is easy to see on the roads, a relation between the increasing traffic and a larger number of bird corpses, dead on impact with the passing cars. Although the collision between birds and cars happens casually, however it is the number of dead birds that is directly proportional to: a) the local density of birds; b) the frequency of passing cars, in relation to the importance of that particular arterial road; c) the model of the straight and flat road, where the speed of the cars is greater; d) the different seasons. Contrary, the number of dead is inversely proportional to the mountain roads, full of bends, where the slower speed reduces the probability of impact. Naturally the number of deaths differs according to the specimens and their ethology, and it's higher for the Passeriformes, that like feeding on the road borders and in the adjacent grounds, especially in winter-time.

This technique has been applied in Sardinia for different models of road (straight, tortuous, etc.); on different altimetry (plain, hill, mountain, etc.); across some different types of botanical associations (cultivations, wood, forest, etc.); and during all the seasons of year. From this study we obtained an approximate idea of density of various bird specimens, in different habitats, during the year.

This method of relative census brings us again to the technique "Breeding Bird Survey", since it is remarked the number of impacts between cars and birds, rather than the visual meeting between the observer and birds.

FRUIT SELECTION BY TROPICAL FRUGIVOROUS BIRDS
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Fruit choice experiments were conducted with captive individuals of several species of small frugivores at the La Selva Biological Station in

tropical lowland rain forest in Costa Rica. We tested preferences for type, size, and ripeness of fruit and for several aspects of accessibility of fruits from perches. All birds tested made repeatable discriminations among the choices offered. Species different in their abilities and preferences corresponding to differences in morphology. Detailled field observations of the foraging repertoire of these species corresponded closely to the abilities and preferences determined in the avian trials.

ECOLOGICAL FOUNDATIONS OF FLOCK-FLYING OF BIRDS
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In 1956-1980 food gathering and flight of 100 000 bird-flocks were studied in the Volga-Caspian region. Based on species behaviour stereotype (mainly on food gathering), flock structure is connected with peculiarities of avian eye structure (angular indeces of vision, keenness of sight etc.). Two transforming classes of flock structure were singled out, composite and linear, each of them changes into the other. Succession of flock construction, their altitude and the number of forms depend on specific peculiarities, the number of birds in the flock and the conditions of flying (altitude, strength and direction of wind etc.). From the point of view of evolution, flock structure developed from initially amorphous (both diffuse and compact) through the stage of strictly composite or linear (or directly from the latter) to secondarily amorphous composite.

BODY COMPOSITION AND METABOLISM IN SPITZBERGEN
PTARMIGAN (L.MUTUS HYPERBOREUS)
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The Spitzbergen ptarmigan is the only herbivorous bird tolerant to the hostile winter of 3 months of continuous darkness, low temperatures and scarcity or even temporary lack of food at the high arctic islands of Svalbard (77-81° NL).

Fundamental for survival in this species is an unusual ability for deposition of fat in the fall when food is readily available. Thus, fat made up as much as from 12-31 per cent of total body weight (reaching 1.2 kg in old males) in early October. In early April when the sun returns, this energy depot is almost drained.

Resting metabolism in this species was the same both in summer and winter, being 75 kcal/kg·day and 120 kcal/kg·day at thermoneutrality and at an ambient temperature of -30°C, respectively.

Assuming that the caloric value of the ptarmigan fat is 9.5 kcal/g the fat deposits in this bird could cover its total energy expenditure at rest and thermoneutrality (above an ambient temperature of -5°C) for 18-39 days. This period could even be further extended if metabolism is depressed during episodes of starvation. Studies of weight change and metabolic response to starvation at different times of the year are currently under way in our laboratory.

## DINAMIK DER NESTAREALE DER VÖGEL DER WESTSIBIRISCHER TIEFEBENE

S.Moskwitin

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Die Angaben des Autors über die 46 Arten, sowie die Veröffentlichungen der letzten 50 Jahre ändern die Vorstellungen über die Nestareale einiger Dutzend Vögelarten, die in erster Linie zu den Spatzen gehören Passeriformes, Fringillidae, Muscicapidae, Silviidae, Turdidae, Emberizidae, Columbidae, Charadriiformes, Rallidae, Falconiformes. Bei den meisten Vögeln war es mit ihrem Ansiedeln verbunden, wobei 6 Arten zum ersten Mal auf dem Flachland zu nisten begannen. Bei den bestimmten Vogelarten (Erythropus vespertinus, Tringa stagnatilis, Columba oenas, C.palumbus, Pseudaedon sibilans, Phragmaticola aedon, Phylloscopus schwarzii) ging das Ansiedeln in einer bestimmten Richtung vor sich, und der wichtigste Faktor war dabei die Veränderung der Umweltverhältnisse außerhalb des ehemaligen Areals, die mit der Temperatursteigerung, der Sukzession der Wälder, den Landwirtschaftlichen Veränderung u.s.w. verbunden worden war. Bei den anderen Vogelarten (Sterna albifrons, Phylloscopus borealis, Corvus frugilegus) war die Nestgebietsänderung in verschiedenen Teilen des Areals zu beobachten, und das Auseinandersiedeln hatte eine radiale Tendenz, die wahrscheinlich mit der bestimmenden Wirkung der endogenen Faktoren und mit den Besonderheiten des Verhaltens der Vögel verbunden ist.

Bei der zweiten Gruppe der Vögel (Podiceps nigricollis, Anatidae, Hydroprogne caspia) ist das Ansiedeln an den neuen Orten mit der Pulsieren des Nestareals verbunden, dessen Maximum früher nicht fixiert worden war. Die meisten dieser Arten gehören zu der Gruppe, die Intrazonenlandschaften besiedeln.

Zur dritten Gruppe gehören wenige Arten (Pernis ptilorhynchus, Accipiter nisus, Limosa limosa), die einen gegliederten Nestareal haben, und von deren Dynamik nur einzelne Funde an den früher unbekannten Orten zeugten.

Der Umfang der Veränderung wird durch die Besonderheiten des Territoriums bestimmt, sowie durch das Vorhandensein der Gebietspopulationen in Westsibirien, die bekanntlich ihre innere Spezifik haben.

## POLYMORPHISM IN THE SYNANTROPICAL COLUMBA LIVIA L. POPULATIONS

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In the peculiarites of their plumage pigmentation synantropical populations of rock pigeons are polymorphous. All in all, 6 coloured morphs are distinguished as a result of survey of 10 000 species (Moskvitin et al., 1981). The rock-coloured (from 12 to 53%) and black-checkered with characteristically marked picture of the wing (from 37 to 84%) pigeons dominated and totally they amounted to 88-98% in each of the eight examined populations. According to the data collected in Tomsk in 1979-1980 (456 copies) the fundamentally morphological, interior and some ecological and ethological characteristics of these morphs were analysed.

Reliable differences between rock-coloured and black-checkered pigeons are established by following indices: adult males differ by the body weight, adult hens - by the length of the body and the relative weight of masticatory stomach. Both hens and males differ by the character of correlations among the above mentioned signs. Among the rock-coloured pigeons there are more under a year hens than among the black-checkered ones. Brooding rock-coloured pigeons are more cautions which was determined by the distance at which they left the nest when watcher was approaching 195 individuals. For rock-coloured nestlings protectively agressive behaviour is often characteristic in the interactions with the watcher. Assortive mating in the rock pigeons wasn't regularly observed every year. Evidently, this is related to the sexual and age dynamics of the populations.

Thus, the rock-coloured and black-checkered morphs are original genetic groups that respond differently to the combination of exterior influences and this determines the dynamics of their correlations within the area.

AKUSTISCHE SIGNALISIERUNG DES FRANKOLINS ( FRANKOLINUS
FRANCOLINUS)IN DER BRUTZEIT

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Es wurde die akustische Signalisierung Frankolins in der Brutzeit untersucht. Man stellte fest, dass der funktionelle Aufbau des akustischen Signalsystems des Frankolins keine prinzipielle Unterschiede vom gesamten für Hühnervögel eigenen Typ hat. Für die Altvögel sind in der Brutzeit Balz-(0.8-3.6 kc), Lock- (0.8-3.2 kc), Fütter- (0.6-2.8 kc) und Warnsignale (1.2-2.6 kc) charakteristisch. Jungvögel haben Orientierungslaute (1.8-3.8 kc), Rufe des Wohlbefindens (1.2-4.2 kc), Weinensignale (1.0-4.5 kc) und Alarmsignale (2.0-3.5 kc). Die ermittelten Besonderheiten des Verhaltens und akustischer Signalisierung können bei der Zucht der Frankoline in der Gefangenschaft ausgenutzt werden. Für die erfolgreiche Züchtung der Jungvögel hat die Stimulierung des Nahrungsreflexes eine besonders grosse Bedeutung. Dieser Reflex wird bei Jungvögeln durch Fütterlaute der Alten stimuliert. Das Vorhandensein bei Jungvögeln der "empfindlichen" Periode(8-16 Stunden nach dem Schlüpfen) und die Fähigket der Jungen akustische Reizmittel einzuprägen ermöglicht nicht nur Signale der Eltern als Stimulierung auszunutzen, sondern auch Monofrequenzsignale im Frequenzgebiet 0.6-1.2 kHz.

HYBRIDISATION OF ROCK PIGEON (COLUMBA LIVIA) AND
EASTERN HOCK PIGEON (COLUMBA RUPESTRIS) IN MONGOLIA
AND COMPARATIVE ECOLOGICAL INVESTIGATIONS

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The geographical ranges of the mostly allopatrically distributed Rock Pigeon and Eastern Rock Pigeon overlap in the southwestern parts of Mongolia. Additional contact zones between the two species exist by the presence of Feral Pigeon in several towns and settlements with in the compact distributional range of Eastern Rock Pigeon. Up to the present no information was

available on morphological and ethological criteria suitable for field identification.

The pattern of tail coloration serves as the main morphological field mark for differentiation of Rock Pigeon from Eastern Rock Pigeon, and from wildtype Feral Pigeon respectively. The voices of both species are easy to distinguish. The synanthropic preference of the species leads to a weakening of ecological isolation and encourages hybridisation. The different phenotypes within the Pigeon population of Ulan-Bator were analyzed. Mixed pairs as well as intermediate individuals were observed. Differentiation of intermediate colour types suggests fertility of the hybrids. However, distribution of the numbers of each type indicates the maintenance of an intraspecific mating preference.

ON THE PLUMAGE POLYMORPHISM IN THE INDIAN REEF HERON,
EGRETTA GULARIS (BOSC)
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The Indian Reef Heron was studied with respect to the plumage polymorphism in the breeding colonies, feeding sites and aviary in Gujarat, northwestern India.

Three morphs, namely, (1) grey without wing patch, (2) grey with wing patch and (3) white are clearly recognisable in the juvenal as well as adult plumages. So called 'intermediate' is extremely rare and of questionable status. 'Lavender' is the juvenal grey in worn out condition.

The frequencies of the grey (with or without wing patch) and white in a population is dependent upon (1) the proportion of fresh water and marine habitats available for feeding (2) extent of gene flow from the neighbouring populations of Little Egret (E. garzetta) and (3) incomplete assortive mating.

The frequencies of the grey and white on a costal strip is related to (1) the substrate structure and (2) timing of the tide cycle.

ABOUT THE URBANIZATION OF BULGARIAN BIRDS
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The question of Bulgarian birds' urbanization has not been investigated yet. At the same time the country's cultured landscape is of great interest, because its territory is a part of the zone of penetration of European,Asian and African fauna urbanization elements. In this report the question of the urbanization of Larus argentatus Pontopp, Streptopelia decaocto Friv,Columba palumbus L., Corvus monedula L., C. cornix L., Pica pica L., Garrulus glandarius L., Apus apus L. and some other species is being examined.

Larus argentatus Pontopp is at its new stage of synantropization, i.e. populating big cities far from the costal area. Columba palumbus L. make its first attempts in building nests in city parks. Streptopelia decaocto Friv. appeared in Bulgaria being fully. shaped a synantropical bird. Together with its expansion to the north before 1970 they populated cities and villages

inside the area. Nowadays more and more often we can observe a reverse phenomenon, i.e. nesting of separate couples inside wild nature. Other bird species also leave settlements. The reason for this antiurbanizational process can be a very high populational density in settlements, a big drop in species' number as a result of real destruction, detriment to forage reserve, shortage of places good for making nests etc. The process of birds' urbanization is as complicated and multilateral as complicated and multilateral is the influence of a human being upon nature. That's why we not always can divine birds' reaction at different stages of landscape's culturing, the ways and scales of urbanization of this or that bird species.

ON FAUNISTIC CICLES: EXTINCTION-EXPANSION-EXTINCTION...
(WITH SPECIAL REFERENCE TO THE EAST PALEARCTIC
DENDROPHILOUS AVIFAUNA)

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Comparision of the present distribution of dendrophilous avifaunas in Siberia and Far East with the natural environment of these territories 19000-16000 years BP (the period of the broadest expansion of the deforested cryoxerophilous landscapes) suggests that forest fauna could not exist over the most part of the regions at that time span. Their formation occurred within the Lateglacial - Holocene, and expanded in a strictly one-way trend from south to north out of adjoining territories of Europe and Inner and East Asia. This indicates a deep faunistic "vacuum" which was a consequence of the large scale extinction of forest (mainly small insectivorous passerines) birds of the fauna of previous interglacial. In Siberia the extinction was determined by considerable destruction of forest refuges in the southern part of the region against a background of very severe, cold and arid,climate 19000-16000 years BP. This phenomenon as yet has no satisfactory explanation for the territory of southern Far East.

It is suggested that in alternation of the stages of extinction-expansion was the most typical mechanism of regional faunagenesis for the East Palearctic dendrophilous avifaunas over the Late and upper part of the Middle Pleistocene. In accordance with the tempo of species turnover, a considerable share of the species is of southern origin, and extinction is mainly of the microfauna (r-selected species), and autochthonous faunagenesis has a negligible role. The history of avifaunas of the studied regions probably differs substantially from that of avifaunas of the Western sector of Eurasia.

SPINAL SOMATOSENSORY MECHANISMS IN PIGEONS

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The afferent fibers of cutaneous receptors (mechanoreceptors, thermoreceptors, nociceptors) project to second order neurons in the dorsal horn of the spinal cord. There is a different projection of thickly myelinated A -fibers and thinly meylinated A -fibers and C-fibers. A -fibers which innervate

mechanoreceptors project primarily to deeper layers of the dorsal horn (lamina IV). Correspondingly both evoked potentials and single units responses have short latencies, and units in lamina IV are generally excited by gentle mechanical stimulation of the skin. As can be seen from evoked potentials and single unit recordings A -fibers and C-fibers project primarily to the dorsal superficial layers of the dorsal horn (lamina I/II). Since both thermoreceptors and nociceptors are supplied with thin fibers, many neurons in lamina I/II are excited by thermal or noxious stimulation of the skin. Some dorsal horn neurons with high spontaneous activity are inhibited both by electrical skin nerve stimulation or by natural stimulation of the skin.

DEATH OF THE HISSING SWAN (CYGNUS OLOR) UNDER
THE CONDITIONS OF ANTHROPOGENIC LANDSCAPE
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"Zhuvintas" Reserve, Lithuanian SSR, USSR

In the period of 1975-1980 the staff of the reservation received 106 reports of hissing swans' deaths on the territory of Lithuania. 68 grown-ups and 38 cygnets (with juvenile plumage) died. The sex structure of grown-up swans is the following: 11 (16.1%) cobs, 8 (11.7%) pens, 49 (72.1%) of undetermined sex. Cygnets' sex was not established. Principal causes of swans' death under the conditions of anthropogenic landscape are: collision with aerial electric conductors (39.8%), predatory animals (19.7%), diseases (10.5%), poaching (9.2%), traumas (3.8%), etc. Collision with aerial high tension electric conductors, telephone and telegraph wires occurs in the spring (March-May) and autumn (September-November) when fledgelings try their wings.

THE FECUNDITY OF THE BLACK-HEADED GULL
(LARUS RIDIBUNDUS) ON LAKE DRUZNO
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The breeding colony on Lake Druzno in northern Poland was studied over a period of four years (1976-1979). Each year, 2-3 test areas (average total surface area 50 m$^2$) were enclosed with suitable wire netting. These areas were so chosen as to include all the habitat types occupied by the breeding colony. Most of this colony of some 4 thousand pairs is distributed on small islands largely overgrown with Solanum dulcamara, while some of the birds also nested among sedges and reeds. All nests in the test areas were marked and the hatched chicks ringed. The test areas were checked every 4-5 days. Chicks were considered to have survived if they reached the age of 25 days. The average number of eggs per pair over the four years was 2.75, while the average number of surviving chicks was 1.39 per pair. Significant differences were found in the breeding success in different types of habitat. This success was least among the pairs nesting in the sedges and reeds, and over the years ranged from 0.13 to 0.56 chicks per pair. The reasons for such low fecundity in these habitats were analysed. Data on the mortality rate of chicks in various stages of their development are given.

PROPOSAL CONCERNING A "SAVING-PROJECT" FOR THE
CRESTED SHELDUCK TADORNA CRISTATA (KURODA, 1917)

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The Crested Shelduck (Tadorna cristata) is only known from 3 museum-spe-
cimen, some observations in the opsn landscape and also from historic Japa-
nese writings and pictures. Obviously it ranks among the rarsst birds in the
world. Since there are no recent observations it is often classified as an
sxtinct species.

All available information concerning this bird (which has never besn com-
pilsd!) permits the following as well as other conclusions: (a) Tadorna
cristata is a tsrtiary boreal duck speciss of East-Asia which was on the
verge of extinction in the ice-age; the only relict ranges exist in Ussuri-
land, Korea and perhaps in NWKNR;(b) In these areas there are still living
several other animal and plant relicts; (c) Tadorna cristata is most probab-
ly still living here. Proof for this: Since about 300 years there have been
about 15 records of the bird, indicating still its existance and rarity
(last in 1964); (d) The extinction of this species in the near future (be-
cause of the incrsasing anthropogenic effects and detrimsntal factors to
their habitats) is very likely; (s) Therefore, in the intersst of worldwide
nature conservation, an attempt towards autecological research as well as
conservation actions for this species should be made.

The following suggestions for an effective "saving-project" for the Ta-
dorna cristata ars addressed to the Nature Conservation Authorities of the
five countries with possible ranges of this duck (USSR, Peoples Republic of
China, both Korean States, Japan):

1. Concentrated search in the breeding and wintering areas (distribution
of colour-leaflets, expeditions etc.);

2. Breeding and reproduction in captivity;

3. Research of Tadorna cristata autecology;

4. Selection and (if possible and necessary) managsment of appropriate
habitats;

5. Reintroduction in the natural area;

6. Legal protection and its execution (national nature conservation acts
and hunting laws, Soviet-Japan Agreement of Migratory Bird-Protection,
Bonn-Convention on the Conservation of Migratory Species of Wild Animals
etc.).

THE THIN EGGSHELL PHENOMENON AND ITS TREND IN THE
WHITE-TAILED EAGLE (HALIAEETUS ALBICILLA), ESPECIALLY
IN THE POPULATION OF THE GERMAN DEMOCRATIC REPUBLIC (GDR)

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Eggshells and shell fragments of the population of Haliaeetus albicilla
in the northern GDR from 1954-1981 were investigated for changes in the egg-
shell parameters and compared with eggshells from 1851-1946, originating

1154

from North-Central Europe (North GDR and present territory of People's Republic of Poland). The recent eggs showed a highly significant reduction of 21% of the previous eggshell thickness. The lowest level was found in the years from 1968-1975. The eggshell thickness of more or less normally reproducting breeding pairs was significantly higher than that of none or poorly reproducing pairs. The thin eggshell phenomenon, caused by DDT/DDE-contamination in the adult eagles, proved to be one of the fundamental factors for the low reproduction of White-tailed Eagles in the GDR. Since 1976 there appeared a significant trend of partial recovery of the eggshell thickness, which is reflecting a decreased biocide contamination in connection with the restricted use of DDT in the GDR and other countries in the 1970s. The statement that putrefaction causes eggshell thinning is discussed. The recent level of shell thickness in the GDR-population of White-tailed Eagles is compared with those from Mongolian People's Republic, Sweden, Finland and Greenland. The importance of investigating the trend of eggshell thickness in Haliaeetus albicilla and other exposed species for biological monitoring (bioindication) of the DDT/DDE-residue level in natural environments is indicated.

THE EFFECT OF CORVID (CORVIDAE) REMOVAL ON
WILLON PTARMIGAN LAGOPUS LAGOPUS POPULATION DYNAMICS

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Nesting and non-nesting corvids (hooded crows Corvus corone cornix, ravens Corvus corax, magpies Pica pica) were removed each year for 4 years (1978-1981) from 4 km$^2$ of willow ptarmigan island habitat for the period just prior to ptarmigan nesting until broods averaged 3 weeks old. Decimation was accomplished primarily by baiting hens eggs with alpha-chloralose. An adjoining area served as a control. Ptarmigan broods were censused on both areas 4 weeks after the mean hatching date and classified as first nest broods, renest broods or pairs without chicks. The proportion of first nest to renest broods and the combined mean brood size did not vary between areas within years. Predation by corvids on ptarmigan chicks was negligible. Success of renest clutches and survival of renest chicks equaled that of first layings. Nest predation in the absence of corvids was attributed to stoats Mustela erminea, the only other predator of ptarmigan eggs on the island. Ptarmigan nesting densities on both areas were similar at the start and finish of the experiment. In conclusion, corvid control during these 4 years was not an effective means of increasing ptarmigan production or nesting densities.

REPRODUCTIVE SUCCESS OF THE BLACK-HEADED GULL (LARUS
RIDIBUNDUS L.) IN THE NORTHERN PART OF BELGIUM

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Reproductive success in the Black-headed Gull (Larus ridibundus L.) was measured during 1978, 1979 and 1980, with individually marked nest in dif-

ferent areas in the Snepkensivijver colony (Lichtaart 51°, 14N; 04° 54E Belgium) consisting of resp. 1400, 1825 and 1560 breeding pairs. In spite of the age of this colony (started 1940), we measured a low mean clutch size of resp. 1.88 (85 nests), 1.90 (1169 nests) and 1.95 (730 nests).

Hatching success in small clutches (1 egg) was significantly lower than in full 3 egg clutches.

There were no significant differences in breeding success between studied areas with different nest densities in the colony.

The overall breeding success was lower when the mean laying date was late in the breeding season.

Comparisons of breeding success and reproduction rate per pair were made with studies already described in literature. These comparisons have shown that great attention must be paid to the method of measuring reproductive success.

The low breeding success observed in our study was specially due to great number of egg losses (41.11%) and low mean clutch size.

SPRING MORTALITY AS A MECHANISM IN REGULATION OF
NUMBERS OF SOME NORTHEASTERN EUROPEAN SONGBIRDS

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Age structure and mortality rates of 6 European passerine species was studied by trapping and ringing at the Rybachy Biological Station in the Courish Spit (eastern Baltic). The study of demographic parameters was based on 298 thousands of migrating birds trapped during 1970-1980. Main data for the analysis were annual fluctuations in numbers of trapped birds, age ratios during fall and spring migration, and the annual mortality rates of adult birds through ringing recoveries. Trapping data during spring showed that proportions of first-year birds in the migrating populations were higher compared with that necessary for the maintenance of stable population density. It was found that the mortality in the period between spring migration and outset of breeding forms 22-50 per cent of the mortality in the whole period between fall migration and outset of breeding. It is suggested that the number of breeding pairs is limited by spring mortality of surplus survivors.

AGGRESSIVE REACTIONS IN MALE OF DOMESTIC AND HOME PIGEONS

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Aggressiveness of male pigeons in wild and domestic individuals was established in 1004 experiments. Pigeon couples were landed on neutral, their own and foreign territory. Domestic male pigeons turned out to be more aggressive than the wild ones (differences were significant at n=814 p=0.01). It is supposed that the differences are due to population density which is much higher for domestic pigeons. High-level aggressiveness for densely-populated colonies is a necessary condition for successful nesting.

## COMPARATIVE GEOGRAPHICAL ANALYSIS OF RAPTOR PREDATION
## IMPACT ON POPULATIONS OF SOME TERRESTRIAL VERTEBRATES

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Raptors of the northern Kazakhstan "island" forests (Naurzum Reserve, 1972-1974 data) exert greater impact on prey populations than those breeding in forests in the south of Moscow Region (Prioksko-Terrasny Reserve, 1976-1979 data). In northern Kazakhstan the rate of raptor predation on total prey populations through summer season was 10-14% of prey number, namely on steppe marmot - 8-10%; microtine rodents - 18-23%; skylark - about 12%; tawny pipit - 7-16%; sand lizard - 5-6%. In the south of Moscow Region the corresponding indices were much lower - 3-6% on microtines, about 3% on small Passerines, less than 1% on woodpeckers, 1-2% on Galliformes, and 1.5% on frogs.

The decrease of principal prey populations was estimated to be an important factor causing the growth of raptor predation rate on additional prey species. For instance, the microtine depression in northern Kazakhstan had determined higher predation upon Passerines, rooks and susliks. The main reason of revealed differences in rates of raptor predation on prey populations on northern Kazakhstan and Moscow Region is in different degrees of complexity and stability of those ecosystems.

## JACKSAW (CORVUS MONEDULA) AND KESTREL (FALCO TINNUNCULUS)
## AS BIOLOGICAL INDICATORS

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Examples of biological indicators can be found in a 18 year investigation in a colony of kestrels and jackdaws near Jena (GDR). The yearly number of breeding pairs, the clutch size and the beginning of the breeding season can be used to characterize the food supply (density of mice - Microtus spec.) prior to and during the breeding season of the kestrels.

Between 1949 and 1957, the number of pairs of jackdaws is dependent on the number of breeding pairs of the predominating kestrels. In the last 9 years anthropogenic influences have changed the population of jackdaws. The decrease in the number of pairs and in the number of young birds per breeding pair indicate the influence of anthropogenic factors.

## FORMES DU COMPORTEMENT REPRODUCTIF DE
## MARTIN-PECHEUR D'EUROPE (ALCEDO ATTHIS L.)

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Dans la région de Saratov, d'apres de contrôle sur cinquante-trois couples d'oiseaux marqués on a déterminé cinq formes du comportement reproductif de Martin-Pêcher d'Europe (Alcedo atthis L.), ci-dessous:

1. Monogamie typique. Les oiseaux ont deux couvées par saison (32 couples).

2. Monogamie à "superposition" des couvées dans le même nid, ce que assu-re trois couvées par saison (4 couples). La femelle pond les oeufs de la deuxième et de la troisième pontes juste après l'apparition des petits de la ponte précédente. C'est le mâle qui couve la 2-e et la 3-e pontes car la femelle élève les oiselets de la couvée précédente. Les deux partenaires élèvent la 3-e couvée.

3. Monogamie à "superposition" des couvées dans de différents nids (la 1-e et la 3-e pontes dans un nid, la 2-e dans l'autre). 6 couples.

4. Bigamie à "superposition" des couvées. La situation est analogique à celle précédente mais la 1-e et la 2-e pontes sont faites par une femelle et la 2-e par l'autre dans un autre nid (5 couples). Alors la 1-e et la 2-e couvées sont élevées par les femelles, la 3-e par les deux partenaires. Le mâle prend part au couvaison do trois pontes.

5. Polygamie typique (en tout, 6 couples: 5 cas de bigamie, 1 cas de tri-gamie). Les femelles couvent parallèlement deux couvées. Le mâle participe au couvaison de la 1-e ou de deux couvées.

Avec le passage de monogamie à polygamie l'efficacité de reproduction augmente (4-6 pontes d'un mâle au lieu de 2 par saison). Il est possible que la polygamie soit conséquence de la prédominance des femelles dans les popu-lations de Martin-Pêcheur (A.D.Noumérov, Y.V.Motukov, 1979).

COMPARATIVE ECOLOGY OF SYMPATRIC LARKS DURING THE
WINTER AND SPRING MIGRATION

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The species of Larks are recorded in Sumbar valley (West Copetdag, Turkme-nia) during the winter and spring migration. Melanocorypha leucoptera and M. bimaculata are rare. Other species are common. Ammomanes deserti, Galeri-da cristata and M. calandra are resident, Alauda arvensis and Eremophila al-pestris are wintering species, Calandrella cinerea and C. rufescens are met on migration only, Lullula arborea breeds. All species have wide similar diets.

Only C. cinerea is strictly isolated from C. rufescens, E. alpestris and A. arvensis by the time of their stay in the region. The majority of species coexist in the same habitats. The greatest number of these syntopic species and the highest density of Larks population are registrated in semidesert hill territories. The species most specialized in choice of foraging sites are separated there by using different feeding microhabitats. E. alpestris prefers steep slopes (inclination is 16-35°), C. rufescens prefers wavy re-lief (steepness of the slopes is 6-16°), M. calandra prefers gently sloping surfaces (inclination is under 5°). Only M. calandra and much less speciali-zed species like G. cristata and A. arvensis prefer the same feeding micro-habitat (gently sloping surfaces).

The foraging behaviour in general is similar in all the species. Simple pecking of food from the ground surface is most common. Specific features of foraging strategies of various species are determined by differences in using less common feeding methods, namely getting food from the ground, vegetable feeding, active pursuit of mobile prey and kleptoparasitism.

## VISIBLE BIRD MIGRATION AND THE SYNOPTIC SITUATION IN THE AUTUMN

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Investigations of bird migrations (1974-1980) in the Kiev Reservoir region do not confirm the leading role of anticyclonic weather upon the visible bird migration dynamics. Cyclones result in the appearance of unfavourable weather conditions for bird migration, nevertheless migrational waves of many diurnal birds (Wood Pigeon, Tits, Buntings, Chaffinch, Bramble Finch, Thistle Finch, Rook, etc.) take place in this situation. Under cyclonic weather, the migration wave of Chaffinch starts. During the period of our investigation, 48 waves have been distinguished. Among them (in 73% of the cases) the barometric pressure during the period of 6 hours preceeding the beginning of the migration on the first day of the wave had fallen, and in 27 per cent had risen. Usually the visible bird migration was poor during anticyclonic weather, except when there was no drop in the temperature. Otherwise, when anticyclones pass through the European territory of the USSR, or by appearing in the rear of cyclones, the intensity of the migration was high. Besides the species mentioned above we have observed the migration of some other species (Diver, Geese, Crane, Lapwing, Song Thrush, Mistle Thrush) the migration of which is correlated with temperature drop.

## DISTRIBUTION, NESTING BIOLOGY AND PROSPECTS FOR CAPTIVE BREEDING OF THE HOUBARA BUSTARD IN USSR

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From year to year the range and number of the eastern subspecies of the Houbara, inhabiting the USSR, are declining. The principal causes of this are destruction of the habitats, growing disturbances, poaching in the nestings areas and unrestricted shooting in the wintering areas.

Now the Houbara survives only in those parts of the USSR that are least of all affected by anthropogenous factors: the northern part of Kaspii lands, south Kasakhstan, Usbekistan, Turkmenia and Tuva. The range of the species everywhere is discontinuous, sometimes dotty, the distribution is mosaic.

The centre of the present day range of the Houbara in the USSR is Usbekistan (Buchara district UzSSR, KazSSR). The number of the Houbara Bustard in unprotected areas is low and varies from 1 bird per 27 $km^2$ to 1 bird per 3.6 $km^2$, on the average - 1 bird per 20-25 $km^2$.

Over the protected areas of the Buchara Persian Gazelle nursery the density of Houbara on the nesting grounds is much higher, than in other parts of the range. The size of the nesting plots of the Houbara is comparatively small (1-1.5 $km^2$), on the protected areas they are found one near another and are even contigious. Disconnection of the spatial links and pairs characterizing the territorial structure of the population in unprotected areas is secondary and caused by a sharp growth of the anthropogenous stress. Peculiarities of the distribution and nesting biology of the Houbara enable

us to envisage a considerable growth of the birds' concentration on areas where they are not disturbed on the nesting grounds. This fact once more underlies the necessity and perspectivity of the creation of the nature reserve to protect the Houbara in USSR.

For the conservation of the Houbara it is necessary to establish the nursery for the captive breeding of this species. The experience of our colleagues abroad and the results of our experiments in the incubation of eggs and raising the nestlings of the Houbara show that this way of preservation of species is feasable. Probably captive breeding of the Houbara followed by the reintroduction of the birds in protected areas is one of the most workable methods of preservation the endangered population of this species.

STRUKTURVERÄNDERNDE FAKTOREN IN DEN TETRAONIDEN-
BIOTOPEN DER OSTSUDETEN (ČSSR)
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Untersuchungen anthropogener Faktoren, Klimas, Vegetationsstruktur, Predatoren- und Nahrungskonkurrenten-Wirkung auf Tetraoniden in Ostsudeten weisen auf die wichtigste Rolle der Biotopstruktur-Degradation in Verbindung mit dem Unruhefaktor auf die Entwicklung dortiger Restpopulationen hin. Vergrasung des Waldbodens mit hochwüchsigen Grasarten, Schwinden von Vaccinium myrtillus und anderer Nahrung oder Deckung mit günstigem Mikroklima bietenden Pflanzen degradiert die Biotopstruktur. Absterbensquote von V. myrtillus steht im ursächlichen Zusammenhang mit zunehmenden Schadstoffimissionen. Beobachtungen über Nebelfrostablagerungen und Schneedecke sowie chemische Analysen der Nebelfrostproben zeigen, dass die Umweltbelastung durch Rauhfrost und Nebel infolge ihres vielfach höheren Schadstoffgehalts grösser als durch Regen und Schneefall ist. Für den Schädigungsgrad der Organismen sind insbesondere hochkontaminierte Niederschlagsepisoden massgebend, deren Wirkung vom jeweiligen physiologischen Zustand und Kondition der Pflanzen und Tiere abhängt. Durch Verbiss und Zertrampeln von Vaccinien, Farnen und Laubbäumen vernichten Cerviden und besonders in Jeseníky-Gebirge eingebürgerte Rupicapra die Nahrungs- und Deckungsressourcen der Tetraonidenarten. Fortschreitende Biotopdegradation durch Immissionen, moderne Bewirtschaftung, überhohen Schalenwildbestand sowie menschliche Aktivitäten haben die in kleinen Gruppen überlebenden Tetraoniden der Ostsudeten Verhaltensänderungen entwickeln lassen. Ausgeprägte Territorialität und Aggressivität an der Reproduktion teilnehmender Vögel ist als Adaptation auf Biotopverschlechterung anzusehen. In restlichen vegetationsstrukturmässig entsprechenden Biotopteilen wurde eine Adaptabilität auf menschliche Störung festgestellt.

POPULATIONAL VARIATIONS IN THE ENERGETICS OF SOME AVIAN SPECIES
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Population characteristics of energy growth expenditurs in Tree Sparrow, Passer m. montanus (L.), Starling, Sturnus vulgaris (L.), Fieldfare, Turdus pilaris (L.) and existence energy of adult birds at different summer and

winter temperatures were studied. Birds for experiments were obtained from
Subarctic, Middle Urals and Khasakhstan regions.

In nestlings of northern populations higher daily energy requirements
with simultaneous shorter growth periods were observed compared to birds
from southern populations. Energy cost of biomass increase in the nestlings
of northern populations was greater than in southern populations due to an
increased energy expenditure on thermoregulation; it fluctuated to a greater
extent. 80% pterilium of subarctic Fieldfare nestlings fledged earlier than
in the Middle Ural ones. Northern nestlings must have earlier energy main-
tainance because it means decrease in heat irradiation. When held under si-
milar captive conditions, adult birds of various populations differed in
autumn and winter in the amount of energy consumed. Comparison of latitudi-
onally distant populations revealed differences in energy input as well as
differences in body mass, reaching 20-30% in Jakutsk, Swerdlovsk and Khasakh-
stan Tree Sparrows.

PSEUDOPHYLLIDEA OF BIRDS IN THE ECOLOGICAL
SYSTEM OF THE BAIKAL

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Composition of species and the infection of birds by cestodes of the Pseu-
dophyllidea order have been established. The Pseudophyllidae order is re-
presented by seven species: Diphyllobothrium dentriticum, D. ditremum, Ligu-
la intestinalis, L. colymbi, Digramma interrupta, D. nemachili, Schistoce-
phalus solidus.

Peculiarities of the biological cycle of Pseudophyllidea (the first in-
termediate hosts are Copepodes, the second ones - fishes) predetermine the
composition of their definitive hosts only of fishivorous birds (Larus ar-
gentatus, L. ridibundus, L. canus, Podiceps cristatus, Mergus merganser,
Phalacrocorax carbo, Gavia stellata). Unfavourable abiotic conditions for
the first intermediate hosts and free-living phase of Pseudophyllidea (co-
racidium), as well as the low size of Cyprinidae fishes in the littoral sys-
tem of the Baikal cause a slight infection of birds and fishes by cestodes
of Ligulidae family. At present there are no pre-conditions for the origin
of epizooties of liguleous and digrammos in the bays of the Baikal. Ecologi-
cal conditions for their outburst may be only in isolated Baikal lakes.

The high infection of sea-gulls by Diphyllobothrium dendriticum is caused
by the fact that their colonies are set in certain regions of the Baikal
(the delta of the Selenga river, the Chivyrkui bay, the Little Sea, the
North-Angarsk bay) and the concentration there of the second intermediate
hosts - fishes of Salmonidea in the period of feeding and spawning migrati-
ons as well. The isolation of the main regions of the nesting of colonial
birds create pre-conditions for forming local populations of D. dendriticum.

ECOLOGY OF THE WHITE STORK (CICONIA CICONIA) IN POLAND
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Information from about 5000 nests occupied by breeding pairs of storks
was obtained in southern Poland in 1973-1981. In 1928, 1934 and 1975,
respectively, 367, 654 and 774 pairs nested in the area of 14.000 sq.km. The
mean clutch size was $4.05 \pm 0.74$ (SD; n=73). Breeding success for all pairs
was 59.1% and for pairs with fledged young 61.4%. Clutch size and breeding
success decreased during the season. A negative correlation was found bet-
ween the density of breeding pairs and the number of fledged young. In 1973-
1981 each pair raised on the average 0.6 chick less than in 1928-1934. The
main reason for the decreased production of young/pair is probably the rise
in the density of White Storks, which leads to the enhancement of intraspe-
cific competition. This is indicated by numerous fights of storks for nests
and by the destruction of broods which results in a increase in the percenta-
ge of such pairs is higher in densely populated regions. Breeding pairs con-
sumed yearly in Poland about 5100 tons ($25.6 \times 10^9$ kJ) and their young about
2720 tons ($13.7 \times 10^9$ kJ) of food, totalling 1.85 kg per meadow and pasture
hectare.

HORMONAL DEVELOPMENT IN MALE ZEBRA FINCHES
(TAENIOPYGIA GUTTATA CASTANOTIS GOULD)
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The morphological and behavioural development of male Zebra Finches is
well known from various investigations. In contrast, however, as for other
small passerine birds, our knowledge about basic processes of the physiolo-
gical development is still rather scarce. The present investigation deals
with the early development of hormone secretion in male Zebra Finches.

The latest state of chromatographical and radioimmunological techniques
allows to separate different hormones even from very small plasma samples
(about 1 ml) and to collect quantitative data on their occurrence and change
over age. Between day 10 and day 70 of life, the development of the hormones
progesterone, dihydrotestosterone, testosterone, and 17 -estradiol has been
followed by consecutive measurements in individual birds (blood samples
being taken every five days). Testosterone development, for example, shows
some remarkable characteristics which are in accordance with the development
of the testes and with some details of the behavioural development (for
example, of song development in the male).

DISTRIBUTION OF HOLLOW-NESTING DURING WINTER TIME
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During winter, the basis of birds population in Kodry forests is repre-
sented by 19 species (density - 715 indiv./sq.km). Common species, such as

Sitta europaea L. (67 indiv./sq.km), Certhia familiaris L. (61 indiv./sq.km),
Parus caeruleus L. (56 indiv./sq.km), Parus major L. (52 indiv./sq.km) toge-
ther with the other hollow-nesting species form multispecies agregations.
Nuthatch and Marsh-Tit accounted for 84% out of total agregations (which
makes 25 to 30% out of total quantity of individuals), respectively Great
Tit and Blue Tit - comprise 65 to 70% and 16%; Tree-Creeper and Woodpeckers
make 35% and 7%. Two types of agregations have been selected. The first type
combines individuals of resident populations into small (up to 15 indivi-
duals) multispecies agregations, distributed mainly on the lower part of
slopes of eastern exposure with preference for oak and ash forests and
utilizing same territory for a few years. In their daily movements, a gene-
ral pattern is followed, expressed in changing the preferred slopes exposure
from eastern and south-eastern towards south with movements up the slope and
back to the place of overnight stay. The second type (up to 22% out of
accounted agregations) is represented by migrants appearing in October in
widely nomadic flocks. Agregations contain 20 to 25 individuals with the
predominance (up to 90%) of one type - Great Tit or Marsh-Tit. When the two
types of agregations meet, mixing of individuals does not occur.

ON THE REPRODUCTION STRATEGY OF THE POPULATION OF
THE COMMON GULL (LARUS CANUS)

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The report is based on data collected in 1962-1980 on colonies of the
Common Gull (making up altogether 212-390 pairs). Every year an average 82%
of the breeding adults and 95% chicks were checked and ringed.

Breeding success was estimated according to the offspring which had reach-
ed sexual maturity and had started nesting. A comparison of the relative re-
production in different age groups enables one to obtain an idea of the re-
production strategy of the population. The relative reproduction is obtained
when the role which a given age group has in the reproduction of the popu-
lation is compared with the role which it itself constitutes in total popu-
lation. It appears that in the first three breeding years, Common Gulls have
considerably less offspring which reach sexual maturity than their own role
in the population, whereas the birds nesting for the fourth and fifth time
produce an amount of offspring which corresponds to their own role in the
population. Beginning with the sixth year of life begins a considerable
amount of overproduction. The Common Gull nests on an average 5.3 times dur-
ing its life-time. Hence the basic role of the population is produced by
fitter individuals of the population whose age exceeds the average age of
the nesting population. It is shown that female birds whose clutches have
lower weights are eliminated at a slightly greater frequency. It is also
shown that the length of the skull of the chicks and the growth rate depend
on egg weight. The Common Gulls reveal an obvious tendency to nest with
partners of their own age. It may be assumed that the offspring of those
pairs possesses a higher biological value where both partners are fitter
(older) than those pairs in which one partner or both partners are less fit.

The probability of inbreeding is small since the tendency of females to return to the birthplace to breed constitutes only 4% (while males have a tendency of 40%). Such a strategy of reproduction is also strengthened by the social-spatial structure of colonies.

THE FOSSIL BIRDS OF CHINA AND SOUTHEASTERN ASIA

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Until recently very little has been known of the history of birds in China and all of Southeast Asia. Most of these early records were of gruiform birds and late Cainozoic forms were those closely related to Struthio if not that very genus, as well as Anatidae and Galliformes, and a few Falconiformes and Columbidae. Ages ranged from Eocene to Recent.

Current field work and analysis of new material has added significantly to this small record, but the oldest fossil birds from Southeast Asia (including the Malay Archipelago) is Eocene.

Recent work by Hou has vastly increased the diversity of Pleistocene birds from China, particularly from Zhongdian, in North China. Yeh's analysis of 4 nearly complete skeletons of a duck (Sinanas, 1980), two phasianids (Shandonggornis, 1977; Linquornis, 1980), and a rallid (Youngornis, 1981) from the Miocene caldera lake deposits of Shanwan, in central China, have given much information on the past history of these groups in China. The gruiform diversity in the early Tertiary has been added to by Hou's report (1980) of a diatrymid-like bird (Zhongyuanus) from the Eocene of western China. Additional new material has been recovered from the Oligocene of western China (Chow et al., 1981) and Pliocene sites in Shaxi, Hebei and Inner Mongolia.

Records in the remainder of Southeast Asia are sparse. Reanalysis of Protoplotus from the mid-Tertiary of Sumatra, however, by van Tets and Rich have indicated that it should no longer be placed in the Anhingidae but in a family of its own rather primitive within the Pelecaniformes.

WHO HELPS WHOM, AND WHY: COOPERATIVE BREEDING IN THE BELL MINER (MANORINA MELANOPHRYS), AN AUSTRALIAN HONEYEATER

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Bell Miners occur in relatively permanent colonies in wet sclerophyll woodlands in southeastern Australia. Their complex social system includes helpers at the nest, with number of helpers ranging from 1 to 10. At most nests, the number of helpers gradually increases with nestling age. Additional helpers may occur during the postfledging period. Helpers (in addition to the male and female) include (a) offspring from previous nests, (b) neighboring males which may not be associated with an active nest of their own, (c) neighboring females, including some which are reproductively active, and (d) occasional 'strangers'. Help may be beneficial to the nesting female by reducing food demands, although females with only 1 helper are capable of renesting as rapidly as those with several helpers. Helpers of recently

fledged young are likely essential to allow the female to renest immediately after a successful nesting effort. The selective advantages of helping to the helper remain speculative. Observations of females copulating with males other than the principal male suggest neighboring males may share paternity in some nests. Mature female helpers are unlikely to be related to the recipient since females generally disperse before breeding. The evolutionary basis of helping for these females may involve an asynchronous mutualism in which helped young will reciprocate by attenting the helping female's offspring.

GEOGRAPHICAL AND SEASONAL VARIATIONS IN THE DIET
OF THE LITTLE OWL IN SPAIN
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We have studied the diet of the Little Owl by examining pellets in each of the three climatic regions of Spain - the humid, the cold Mediterranean, and the Mediterranean proper. The feeding spectrum is quite wide, ranging from mammals heavier than the predator to ants of 0.01 grams. Coleopthera are the commonest prey item, but the greatest biomass is obtained from vertebrates, especially the rodents. The analyses show that the diet has great geographical variation, and on a lesser scale, seasonal and even local changes.

We consider two basic zones: the Mediterranean, characterized by a preponderance of Reptilia, Coleopthera and Orthopthera; and the cold Mediterranean and humid, whose common features are the importance of Microtinae, birds and Insectivora. As for seasonal differences, the energy input of the vertebrate prey is greatest in the spring and least in winter, which is when Orthopthera become important. Among rodents, the Microtinae are typical prey in springtime.

These variations seem to suggest more the existence of different availability of prey in the several ecosystems than to selection of prey, as shown by the high values of trophic diversity, and the correlation of these with latitude and with different groupings of prey.

ADAPTIVE ORGANIZATION OF TERNS COLONIES
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During 10 years I have studied 80 colonies and 15000 families of several species: Sterna hirundo; S. paradisaea, S. aleutica and S. albifrons.

By the term "adaptive organization" I mean the unity of defensive and dynamical properties of colonies. The observations indicated that functions of families and properties of colonies depend on the distance between two closest neighboures, position of nest site in a colony, size of a colony and ecological inertia. The term "ecological inertia" is used to determine the ability of birds to oppose external influences. Other things being equal, the formation of colonies is always followed by the decrease in rate of defensive and dynamical processes and by the increase of ecological inertia of birds.

It is of great importance to know the ratio number of peripheral versus centre families (K.). The colonies can readily be subdivided into three main groups: small (K<1), medium (K=1), large (K>1).

It has been generally assumed that the most active defence of nests is in the centre of a colony. My results reject this view. The best defence has always been near the edge of colony. And the lowest death-rate of chicks in the centre is only the result of such a behaviour.

## SPATIAL DISTRIBUTION (CARTOGRAPHIC ANALYSIS) OF THE BIRD POPULATION OF SOUTH EAST TURKMENISTAN

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The ornithographic mapping of the area of 87.3 thousand square kilometres was carried out. It covered the Tedjen-Murgab interstream and the adjoining areas of the Karakum desert during the spring period of 1975-1978. Birds were counted from a moving automobile along the zones of vision (5764 km in all). 52012 individuals of 186 bird species were counted.

Sandy habitats include 47 species on the average, having a density of 64 species per square kilometre. Dominant species turned out to be Passer indicus (on the average 30.7% of all species), Galerida cristata (20.4%), and on some sandy areas - Podoces panderi (9.4%), Calandrella cinerea (8.3%) and Calandrella rufescens (8.3%), Hippolais rama (7.5%) and Hippolais languida (7.5%). In clayey habitats 33 species were observed, that is on the average 55 species per square kilometre. Galerida cristata (41%), Calandrella cinerea (12%) and Calandrella rufescens (12%) dominate. 40 species on the average fall on sandy loam-loess habitats, their density coming up to 153 species per square kilometre. Galerida cristata (29.1%), Oenanthe isabellina (12.1%) and Melanocorypha calandra (6.7%) make up the background of the bird population. In the oases along the Tedjen and Murgab river valleys the number of registered species comes to 53, having a density of 173 species per square kilometre on the average. The dominant species in the oases are Passer indicus (29%), Streptopelia turtur (14%), Pica pica (8.1%), but in the settlements the dominant species is Passer montanus (42%).

## CHANGES IN MIGRATIONAL BEHAVIOUR OF THE GREAT TIT

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The results of 14 years' period of work (1967-1980) at the station of Pape (the extreme south-west point of Latvia) showed that in comparison with the investigations of 1954-1962 (Veromann,1965) the Great Tit occurred more often and regularly in the Baltic area during its autumn migration. It has been found that the start of migration, which previously fluctuated considerably, is stable now and occurs earlier. The number of birds participating in migration has increased as well as their flocks. Migration of the Great Tit, obviously, has acquired a more regular and mass character in the last decades. Possibly it has been caused by a general increase in bird numbers due to a greater amount of artificial nesting sites.

TROPHIC NICHES OF PASSERINE BIRDS IN SUBARCTIC, "THE
GAUSE'S PRINCIPLE" AND NORTH ECOSYSTEMS RESISTANCE

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According to dominant competition theory, species which have common habitats and similar food must have different localization of feeding areas. Contrary to this our investigation of Phylloscopus trochilus and Ph. borealis in the north tajga of Ural in 1977 shows almost complete foraging niches similarity in its common habitat conditions. Feeding behaviour was studied under favourable weather conditions and under abrupt cold periods in South tundra of Yamal in 1980. Distant taxonomic species Ph. trochilus (Sylviidae) and Emberiza pusilla (Emberizinae) which also lived here and fed their chicks similar food were used for comparison. Niche breadth and overlap were defined by standard formulas (Hubert, 1978). The overlap was quite large along all seven dimensions. Under change for the worse feed conditions, niches of both species narrowed, however overlap coefficient increased. The species reacted to change in the feeding conditions in the same way. High trophic plasticity is a property of the majority of species of Subarctic birds. It is necessary in unstable existence conditions. Ecological polyfunctionality of species secures counterpart relations in ecosystems with a low species diversity that is important to increase its resistance from disturbances. A possibility of trophic counterparts coexistence may be explained by presence of energetic reserve in ecosystem, which turns on under unpredicted climatic disturbances. Many facts contradicting to Gause's principle of competition exclusion are also known in other zones with unstable climate.


VARIABILITY OF THE NESTING DENSITY OF THE PASSERINE
BIRDS ON THE OB FOREST-TUNDRA

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For the ten years (1970-1979) on the territory of the forest-tundra station "Harp" the nesting of 17 passerine species of birds occured. The "Harp" area has 270 ha. Ten species nested each year here. Their nesting density was very variable. Motacilla alba had the comparatively constant density only. The variability of the nesting density of Anthus cervinus was 3.7, Motacilla flava - 3.8, Emberiza schoeniclus - 3.9, Phylloscopus trochilus - 4.3, Anthus pratensis - 6.6, Calcarius lapponicus - 10, Acanthis flammea - 20 times. One half of the species which have a northern border of breeding area in station region nested irregularly here. The second group of the species have a northern border of breeding area to North or to South. Between these species of the nesting irregularity is below two times. Mean nesting density of numerous birds varied less than in not numerous species for ten years. Apparently, it is bound with their territoriality, which establish the upper density level of numerous species.

SPATIAL AND SEASONAL DISTRIBUTION OF 'DERMATITIS', A DISEASE
OF OYSTERCATCHERS ON STOKHOLM AND ITS ECOLOGICAL EFFECTS

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'Dermatitis' is a viral disease of Oystercatchers, presumably akin to
Puffinosis. Its symptoms are blisters, usually on various parts of the feet,
and partial paralysis. It affects mainly chicks for which it is usually
lethal, but also adults that often recover.

During a long-term population study on Stokholm Island (1963-1978) it was
found that the spatial distribution of the disease on the island was not
random. Rather, diseased birds occurred in contiguous territories, concen-
trated around relatively wet areas, which provided better feeding conditions
than the drier areas. In the infected areas disease affected young hatched
early in the season in a significantly greater frequency that young hatched
later. It is proposed that the Oystercatcher's exposure to this disease is
associated with its relatively new habit of utilizing terrestrial habitats
for young-raising; the activity of the vector is presumably associated with
moisture, which declines later in the season.

Usually, early-breeding Oystercatchers are more successful in raising
young than others. But in terrestrial feeding individuals, a selection
against early breeding may be now operational.


NICHE SHIFTS OF BIRDS IN MAN-MADE ENVIRONMENTS

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Species diversity, average niche breadth, average niche overlap and niche
shifts of three dominant species, great tit, blue tit and tree sparrow, were
compared for oak forest, acacia woodland and urban park, as well as for
various tree species within the park. The survey was based on records of in-
dividual birds feeding in various macrohabitats during the breeding season
and winter.

Bird diversity was lower in the urban park, with its mixed tree species,
than in homogeneous oak forest, but higher than in homogeneous acacia wood-
land.

Average niche breadth and niche overlap were assessed using formulae
suggested by Pilou for standardized measures (E.C.Pilou: Ecological Diversi-
ty. 1975. New York, p. 135-142).

During the breeding season, average niche breadth and niche overlap were
lower in the urban park than in oak forest, but they were lowest in acacia
woodland. It might be supposed that the decrease in number of breeding spe-
cies is consistent with increased segregation of species in the poorer and
poorer man-made environments. However the niche breadth of the great tit
and blue tit decreases (oak forest > urban park > acacia woodland) without
increasing their segregation because their niche overlap is greatest in the
urban park, with acacia woodland next, and the lowest value in oak forest.
This suggests that competition between these two species increases in the

man-made environment during breeding season. The niche breadth for the tree sparrow is highest in urban parks, where the greatest niche overlaps between tree sparrow and great tit, and tree sparrow and blue tit also occur.

In oak forest and acacia woodland, when temperatures are between -1°C and -10°C, and the soil is covered by snow, the average niche breadth and niche overlap are lower than when temperatures are between 0°C and +10°C, without snow. This situation is reversed in the urban park. In severe weather the urban environment is advantageous for the winter bird population, but without the evolutionary divergence of these species, interspecies competition increases.

INVESTIGATIONS ON REPRODUCTIVE PERFORMANCE OF THE LITTLE
TERN (STERNA ALBIFRONS)
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The secondary fertility has been analyzed in relation to various extra- and intrapopular factors for a colourringed population on the southern coast of the Baltic, consisting of avg. 41 (23-54) breeding pairs, which have been investigated since 1973 on size determining mechanisms, etc.

Reproductive maturity is achieved at an age of avg. 3.0 years (n=44). Eggs are laid in an interval of avg. 1.7 days (n=147), main laying period 16.5 - 10.6 days. Hatching takes place (19-23 days thereafter and 3 weeks later the young birds fledge. After loss of a clutch or early death of the chicks, up to 3 additional clutches may be laid, possibly following resettlement of the breeding pair as far as 150 kms away from the original nest site.

Totals per female avg. 1.7 (initial and additional) clutches (n=611) with each 2.25 eggs (n=1375; = 3.7 eggs per female) have been registered. Initial clutches with 2.54 eggs are clearly larger as the subsequent ones. First breeding females are producing fewer eggs (avg. 2.3; n=10) in initial clutches and rarely have additional clutches.

Of the total number of eggs 28.6% (= 1.10 per breeding pair) were hatched. Most losses were caused by predators (78%), flooding (6%) and human activity (7.5%). Among predators, foxes and large gulls played the most important part. They may destroy all offspring in some locations or in particular years. In 1975, 45 breeding pairs laid 160 eggs in 92 clutches, none of which hatched. The number of fledging birds is also determined particularly by predators, but also is affected by the weather.

The results lead to the conclusion that reduction of fertility caused by predators is a key factor in population dynamics of this threatened species.

ÖKOLOGIE UND SCHUTZ DES STEINKAUZES,
ATHENE NOCTUA, IN DER DDR
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Bis zur Mitte dieses Jahrhunderts gehörte der Steinkauz, Athene noctua, zu den häufigsten Eulenarten auf dem Territorium der DDR. Danach erfolgte eine starke Bestandsabnahme, so daß die Eule heute zu den "vom Aussterben bedrohten Arten" gehört und besonderen Schutz erhält. Dafür sind Untersuch-

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ungen über Habitatansprüche, Ursachen des Rückganges und die Erarbeitung
eines Artenschutzprogrammes dringend erforderlich. Diese Schwerpunkte werden
nachstehend dargestellt.

Habitatansprüche: Von Großvegetation weitgehend freie ("offene" Landschaft),
artspezifische Jagdmöglichkeiten (keine geschlossene Gras- und Krautvegeta-
tion). Dadurch Möglichkeit zur Bodenjagd, Vorhandensein relativ niedriger
Ansitzpunkte (Koppelpfähle, Steinhaufen u.a.), kontinuierliches Nahrungsan-
gebot in Form von Kleinsäugern, Vögeln und Insekten auf begrenztem Raum,
Einstands- und Brutplätze wie höhlenreiche Baumbestände, Baue erdbewohnender
Säuger, oder verfallene bzw. von außen zugängliche Gebäude, gemäßigter Klima-
bereich, geringer Feind- und Konkurrenzdruck.

Ursachen des Rückganges: Lebensraumzerstörung, verstärkte Verluste, kli-
matische Faktoren, Biozide, Feinde und Konkurrenzdruck.

Artenschutzprogramm: Schutzmaßnahmen für artspezifische Habitate (Erhalt-
ung von Brut- und Einstandsmöglichkeiten und Nahrungsräumen), systematische
Vergrößerung von Restpopulationen (Anbringen von Niströhren), Schutz der
Brutplätze vor Raubwild, Raubzeug und Ratten, Pflegemaßnahmen geeigneter
Höhlenbäume, Anpflanzung geeigneter Holzarten, keine Förderung des Waldkauzes
durch Nistkästen, in Brut- und Nahrungsrevieren Einsatz von Bioziden zwischen
Naturschutzorganen und landwirtschaftlichen Betrieben exakt abstimmen.

Place of employment: Sachsen und Thüringen, DDR.

## THE INHERITANCE OF SOCIAL DOMINANCE IN BEWICK'S SWAN (CYGNUS COLUMBIANUS BEWICKII)

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In Bewick's swans, the social dominance of cygnets during their first
winter of life is closely related to their parents' dominance. This is a
result of parental protective behaviour, which cygnets solicit as soon as
they are threatened by an opponent. However, this 'inheritance' of dominance
is not confined to the first winter. Evidence from longterm records of indi-
viduals and their offspring at Welney Wildfowl Refuge, Norfolk, suggests
that offspring of highranking parents are themselves high-ranking as adults,
and offspring of low-ranking parents are low-ranking as adults.

## PHENOLOGY OF SPRING MIGRATION IN UKRAINE

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An analysis has been made of the phenological observations on bird migra-
tion in Ukraine in 1975-1981 and of abundant literature data of similar in-
vestigations. Since 1843 phenological observations of migration of more than
100 species in Kiev region were carried out. As a result many years' average
dates of birds' arrivals and their variations were established, four "coming
waves" were ascertained, a wide variation of the arrival dates in first
spring migrants were discovered and a tendency of definite changes was es-
tablished. In one group of species (Starling pattern) average dates were
earlier, in a second group (House Martin pattern) - average dates were late

and in others (White Stork pattern) - no changes. The positive and negative pair correlation in dates of arrival between species has been discovered as well.

The observations of the numerous correspondents offered an opportunity to draw a map of arrival of eight species in Ukraine. According to curves of isophenological line, three migration ways are clear. The first lies over the northen districts of the Ukrainian SSR from the west to the east. The second goes from the south-west to the north-east across the complete territory of the republic. And the third one lies along the coasts of the Black and Azov Seas. Besides this, the map shows how the birds avoid the Carpathians early in the spring, going arround the main chain of the mountains.

Geographic variation analysis of the arrival dates of Starling, Geese, Sky Lark, Golden Oriole, Nightingale Thrush and some others shows that the dates of their arrivial in the northern regions varies minimally compared to species that arrive late in spring in south regions.

COMPARISON OF THE SOCIAL SYSTEMS OF SEVEN SPECIES OF
DUCKS IN THE GENUS ANAS
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Aspects of the ecology and behaviour of seven species of ducks in the genus Anas were studied from 1968 to the present in an attempt to describe and contrast the social systems of each species. The Mallard (A. platyrhynchos), Pintail (A. acuta), Gadwall (A. strepera), Wigeon (A. americana), Shoveler (A. clypeata) and Blue-winged Teal (A. discors) were observed in two habitats in southern Manitoba, Canada. The Black Duck (A. rubripes) was studied in three habitats in northeastern Nova Scotia, Canada. Data was collected on home range size, territory parameters, pair bond strength, tenure and duration, and other aspects of the breeding biology of pairs. Data was also collected on the behavior of unpaired males and on interactions between pairs and unpaired males. The seven species represent a continuum with regards to these ecological and behavioral characteristics. For example, the Pintail has the largest home range, is not territorial and has a poorly developed pair bond. The Shoveler is the other extreme and defends a well-defined territory, on a small home range and has a strong pair bond. The various ecological and behavioral characteristics of each species are discussed and each species is placed relative to the others in the continuum.

CONTAMINATION OF WATER SUPPLY BY GULLS,
AND A SOLUTION
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Concern has been mounting in recent years over the role of gulls (Larus sp.) as dissemenators of potential human pathogens. During the last ten years the level of bacterial contamination in two service reservoirs in the west of Scotland, during the winter months, was high and was correlated with the numbers of gulls using these reservoirs as nocturnal roosting sites.

The roosting gulls were predominantly Herring gulls (Larus argentatus) though numbers of Blackheaded gulls (Larus ridibundus) and Common gulls (Larus canus) were also present.

Attempts were made, using taped distress calls of these three species of gulls, broadcast over the reservoirs, to disperse this roosting population of gulls in 1980/81 and 1981/82.

The results show that there was little habituation of the gulls to the taped distress calls and a dramatic improvement of raw water quality due to the dispersal of the gulls to alternative roosting sites. The effectiveness of these behavioural scaring techniques with respect to local climatic conditions and species composition of the roosting flocks is also considered.

RELATIONSHIPS BETWEEN RAPTORS AND MICROTINE RODENTS IN
AGRICULTURAL AREAS OF PERM REGION.
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During the years of 1976-1979 the population of 10 raptor species (mainly rodentivorous predators) fluctuated rather synchronously with that of their prey - microtine rodents. The most considerable fluctuations were a function of population of such common species as the Buzzard (from 2.5 to 12.2 pair per 100 sq.km), the Kestrel (2.5-11.9) and the Long-Eared Owl (3.2-6.8).

In rodent peak years all the raptors, which had arrived in the study area, began to breed. Predominant food items in their diets were microtine rodents, mainly the common vole (from 49.7% of Eagle Owl's to 94.7% of Short-eared Owl's total prey). In the years of decline micro-rodent population there occured specific and individual reactions of raptors to the lack of food. For instance, some Buzzard individuals abandoned their breeding area some time after their arrival, others did breed, switched over to a wide range of other food sources (birds, amphibians, reptiles,etc.), some pairs continued to feed on scarce common voles, without even making any attempt to breed.

Clearly-observed preferable prey were pregnant females (36.1% of total prey versus 13.8% from rodents' count data). Raptors more often preyed on adult individuals (from 62.3% for Tengmalm's Owl to 80.2% for Buzzard); no preference for male or female prey was discovered.

STUDIES IN GEOGRAPHIC ASPECTS AND INTERASPECTS
OF THE ACOUSTIC-REPELLENT IMPACT ON BIRDS IN
DIFFERENT REGIONS OF THE USSR
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From 1978 to 1981 the geographic aspects and interaspects of the acoustic repellents' impact on birds characteristics of most coastal and inland air-fields (Corvidae, Laridae, Sturnus vulgaris) were studied. The research covered Lithuania, the Baltic, Black Sea and Caspian coasts, Soviet Central Asia, Chukot and Kamchatka peninsulas and the Island of Bering.

Local birds were subjected to acoustic repellent relays recorded from these and other species but in geographically remote areas.

About 1500 relays were analysed. The studies indicated that no geographic aspects of the acoustic repellent impact were manifest for Corvidae, Laridae and Sturnus vulgaris while the geographic interaspects of the acoustic repellent impact were manifest both among congeneric species and systematically remote and depended on ecological relations of birds within a concrete biotope.

## STATUS OF GRUS JAPONENSIS AND G.VIPIO POPULATIONS
## IN PRIMORYE TERRITORY

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Two regions of vital importance for G. japonensis and G. vipio are known in Primorye. Khanka lowland is a place of regular breeding and the Tumannaya river mouth (southern Primorye) is the place of regular stations during migrations.

There are three isolated sites of nesting in Khanka lowland: Ilistaya river mouth (3-t pairs of G. japonensis and 1-2 pairs of G. vipio); bogs on the north-east part of Khanka (about 15 pairs of G. japonensis and 3-4 pairs of G. vipio); upper reaches of Chornaya river (6-8 pairs of G. japonensis). The following results of aviacensus (August of 1980) were obtained: 116 speciments (18 juv) of G. japonensis and 8-10 specimens of G. vipio; about fourth one of Grus japonensis of the world population probably inhabits the Khanka basin (including birds occuring on China territory).

More than 100 specimens of G. japonensis and about 200 of G. vipio stayed annually during spring migration over the marshy area of the Tumannaya river mouth scarred with numerous mostly salt waters. G. japonensis arrives in early March and stays at the lowland till late March-early April. G. vipio migration was observed in late April. In spring the main forage of G. japonensis is dead fish, mostly Carassius auratus. In autumn the birds migrate by transit.

## FAUNA AND THE RELATIVE NUMBER OF RAPTORS IN ZABAIKÁLIE
## (EAST OF BAIKAL)

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In the period of 1959-1979 32 species of raptors have been recorded in Zabaikalie including 20 nesting and 7 supposedly nesting species.

Total number of raptors in summer season was on the average 1.7 individuals per 10 km of route (from 0.3 to 4.0) over open habitats and 1.3. individuals per 10 km of route (0.3-4.7) over forests.

Dominanting species were Buteo buteo (0.4-2.0 individuals per 10 km of route), Milvus migrans (0.3-3.0), Accipiter nisus (0.1-3.3). Circus cyaneus (0.1-1.3), Falco subbuteo (0.2-1.2) and Falco tinnunculus (0.1-1.2). Sometimes great flocks (up to 137 individuals) of Milvus migrans (probably bachelor-males) were recorded.

INTERRELATION BETWEEN THE COMPONENTS OF VERNAL
MIGRATORY STATE IN CHAFFINCH AND BRAMBLING
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The analysis of vernal migratory orientation experiments in chaffinches
and bramblings in automatic round cages at the Kurische Nehrung shows diffe-
rent correlations between the fat reserves level and migratory behaviour at
the end of the migratory phase and similar relations of these components in
the middle of migratory period. When birds of both species have precise
vernal migratory orientation (for chaffinches n=380, for bramblings n=260),
a positive correlation has been established between fattening, activity rate
and orientation power (vector length). Correlation value for the fat reserv-
es level and activity level in the chaffinches was $0.73 \pm 0.12$, in bramblings
$0.71 \pm 0.14$; for the fat reserves level and vector length $0.69 \pm 0.09$ and
$0.51 \pm 0.12$ respectively. At the end of migratory period, precise orientation
occured in birds with low fat reserves; fatty birds often had poor orienta-
tion. It indicates and independent regulation of different migratory state
components by internal and external stimuli.

FORMATION AND FIDELITY OF PAIRS IN POPULATION OF RINGED
PLOVER (CHARADRIUS HIATICULA)
Axel Siefke
Vogelwarte Hiddensee, Kloster/Hiddensee, GDR

The composition of pairs according to origin and age of mates as well as
their fidelity resp. their replacement during breeding time and from year to
year has been analyzed for a colourringed population on the southern coast
of the Baltic, consisting of avg. 34 (24-42) breeding pairs, which have been
investigated since 1974 on size determining mechanisms, etc.

Adult birds faithful to breeding area appeared singly or in pairs in
26.2/49.8% of the pairs (n=237), first breeding birds faithful to their
birth place in 11.8/2.5% and (unringed) newcomers in 26.2/15.6%. The age
difference between the mates may be up to 9 years, in average it was 1.5
years (n=95).

Of the 61 males, which have bred more than one year (avg. 3.5 years;
n=153) in the area, in 88.2% of cases the old territory was reoccupied and
in 46.4% the pair bond from the previous year was maintained. A change of
the female (22.9%) occured particularly in territories of inferior quality
as well as in the case of change of territory of the male from one of poor
quality, to a better one.

Losses of mates during breeding are compensated immediately. In case a
female is lost (rarely) still unmated older or (mostly) first breeding com-
pensating mates of the male remaining in the territory appear, in experiments
up to 5 females per male. In contrast, the females resettle in case the male
is lost and mate at other localities with territorial (mainly first breeding)
males.

The discussion concentrates mainly on the population-ecological consequen-
ces of the settling behaviour and the importance of the so-called popula-
tion reserve.

THE ROLE OF GULLS IN TROPHIC CHAINS OF GROUND
AND WATER ECOSYSTEMS OF THE NORTH-WESTERN
BLACK SEA COAST

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If a species is a member of the land and/or aquatic ecosystems influences these biocenose considerably. Three groups can be determined on the basis of their feeding biotope, namely: (1) Feeding in aquatic ecosystems (Larus ichtyaetus Pall., Hydroprogne caspia Pall., Sterna sandvicensis Lath., Sterna albifrons Pall.); (2) Obtaining food on seaside steppe (Larus melanocephalus Temmi, Gelochelidon nilotica Gm.); and (3) Feeding in tenestrial and aquatic ecosystems (Larus argentatus Pontop., Sterna hirundo L.).

Gulls influence separate links differently in trophic chains of the ecosystems under study. The greatest number of connections are formed according to block saprotroph components (38.3%), and a smaller number of connections to zoophages (22.5%) and to phytophages (21.6%). Participation of gulls in biotic cycles was studied from both sides - as uses of biological production and as a source of biological products. In general, trophic connections were formed with respect to components of aquatic ecosystems.

In aquatic biocenose, the ecological chains are closed because the products of birds (excreta, carcasses) end in the water. These influence primary production. Other trophic links are formed by primary productions; gulls are the lost link. In this case, cycling of materials occurs within a single biotope.

In terrestrial biocenose, biotic transfer occurs mainly in one direction from land to water. Although some birds feed in terrestrial biotopes, the products of their vital activity reach bodies of water.

Because these birds participate in food chains of aquatic ecosystems, they are links between terrestrial and aquatic biocenose.

NEAR WATER BIRDS OF THE ECOSYSTEM OF THE LARGEST ASIAN
LAKES (ON THE EXAMPLE OF THE LAKE BAIKAL, THE USSR AND
THE LAKE KHUBSUGUL, MPR)

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The lakes Baikal and Khubsugul are the deepest natural water-reservours of Asia. Connected by the Selenga system they differ from each other only in size and in their situation above the sea-level. On the lakes 95 species of near-water birds were registered (Gaviiformes - 2, Podicipediformes - 4, Pelecaniformes - 1, Ciconiiformes - 4, Anseriformes - 30, Gruiformes - 5, Charadriiformes- 49). Out of this number 67 species nest on the lakes (Baikal - 64, Khubsugul - 40). Near water birds make up 27% on the ornithofauna on the Baikal and 29% on the Khubsugul. Because of their great population this group of birds plays a noticable part in the functioning of the lakes' ecosystem.

37 species are common for the lakes (the most typical are Gavia arctica (L.), Podiceps nigricollis C.L.Brehm, P. auritus (L.), P. cristatus (L.),

_Ardea cinerea_ L., _Ciconia nigra_ (L.), majority of Anseriformes and Charadrii-
dae, Chlidonias and Sterna, Larus). On the Khubsugul only 3 species which do
not nest on the Baikal were found (_Phalacrocorax carbo_ (L.), _Eulabeia indi-
ca_, _Tringa totanus_ L.) whereas on the Baikal 17 species which were not re-
gistered on the Khubsugul were noted (_Gavia stellata_ (Pontopp.), _Podiceps
griseigena_ (Bodd.), _Botaurus stellaris_ (L.), _Cygnus_ _cygnoides_ (L.), _Mela-
nitta deglandi_ (Bp.), _Anas falcata_ Georgi, _A. acuta_ L., _Aythya ferina_ (L.),
_Historionicus histrionicus_ (L.), _Mergus serrator_ L., _M. albellus_ L., _Calidris
subminuta_ (Midd.), _Limosa limosa_ (L.), _L. canus_ L., _Hydroprogne caspia_
(Pall.), _Chlidonias hybrida_ (Pall.).

Both lakes, especially the Baikal, due to the mountainous character of
extensive territory surrounding them are the places of near water birds con-
centration - birds both on flight and nesting. Birds distribution along
their littoral is also irregular: the main part concentrates in the outfalls
of big tributaries, on shallow sections and on marsh-ridden plains. Numbers
of lamme-lirostrals on the Baikal in such places reaches from 200 to 400
nest per 100 ha of areas suitable for nesting, and the total numbers of
Larus, nesting on the Baikal reaches 22-25 thousand, Chlidonias and Sterna -
40-45 thousand. On the Khubsugul the nesting population of _Larus argentatus
Pontopp._ is 4 thousands of birds. The main factors determining the number
and distribution of aquatic-marsh birds are the seasonal and interannual
changes of water level of water-reservoirs and the anthropogenic effects
which have lately considerably increased.


THE IMPRINTING OF THE NEST TERRITORY
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The analysis of the data of the birds nesting at the Kurishe Nehrung re-
vealed that most of the one-year-old individuals of the _Fringilla coelebs,
Sylvia nisoria_, _Phylloscopus trochilus_ ( 90 % ) and some of the _Hippolais
icterina_, _Lanius collurio_, and _Carpodacus erythrinus_ ( 26 % ) returned to
their birth site in the following years. Most of the _H. icterina_, _L. collu-
rio_, and _C. erythrinus_ returned to another territory, which they inhabited
after they left the birth site.

Young _F. coelebs_ and _S. nisoria_ imprinted on the territory of the future
nesting during the "sensitive period" of an age between 30-40 days, before
the beginning of the intensive postfledging movements. The imprinting of the
nest site of most _H. icterina_, _L. collurio_ and _C. erythrinus_ took place im-
mediately after they left the birth site, at the age of more than 30 days.

The formation of the site tenacity to the nest territory in migrant birds
took place at juvenile age. It was characterized by the existence of a reli-
able "sensitive period" for imprinting. Reasons exist to support the conclus-
ion that site tenacity of these species is the result of imprinting.

# NESTING OF THE SIBERIAN CRANE IN WEST SIBERIA

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For more than a hundred years after the Siberian Crane was described the breeding places of its western population remained unknown. In 1981 special investigations were undertaken. Aerial surveys were performed over the territory of more than 30 000 $km^2$ between 63°-67° of North in the low Ob region.

On the 14-th of June in the region of the right tributary of the Ob river - the river Kunovat - 5 pairs of the Siberian Cranes were discovered. The birds held to the edge of a large (about 200 $km^2$) bog area with numerous lakes among the larch forest of the northern taiga. The minimum distance between the nests of this group was 1.5 km, the maximum - 10 km. On the 16-th and the 25-th of June 3 more pairs were discovered on raised bogs to the north from the river Kunovat. For 5 of the 8 discovered pairs breeding was proved. Two of the four carefully examined clutches contained 2 eggs, and 2 clutches contained 1 egg. The nests were situated on up-raised sphagnum bogs close to the border of the depressed larch forest. They were open nest on moss covered hillocks or ridges with rare larches and birches. Common Cranes were found breeding (4 nests) together with the Siverian Cranes in the same habitats. In two cases the nests of the two species were in less than a 1 km distance from each other.

On the 25-th of June in one of the Siberian Cranes' nests a chick hatched, two other pairs judging by their behavior had already had chicks. The eggs were apparently laid in the last week of May, when the first patches of earth appeared on the snow-covered surface.

The behavior of these birds in the vicinity of the nests differs from the behavior of the Jakutian Siberian Cranes. The cranes stayed on in their nests when the airplane was quite low. Often after leaving the nests the frightened birds did not fly away, but tried to hide under trees and fairly soon returned to their nests. A similar reaction was observed among the Common Cranes.

# ON BIOGEOCENOLOGICAL TYPOLOGY OF CESTODES OF HYDROPHILOUS AND LAND BIRDS

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Five main biogeocenological types among the helmints of the vertebrates such as the primary hydrobionts, the primary amphibionts, the primary atmobionts, the secondary amphibionts and the secondary hydrobionts can be pointed out judging by the nature of ecological links and also taking into account their evolution. Among the cestodes of the birds one can distinguish helmints of three types:

I. The primary amphibionts - their larvas develop in the organism of the water invertebrates and the fishes, while the nature forms develop in the intestine of hydrophilous birds. These are Liguilidae (Ligula, Digramma, Schistocephalus), some of Diphyllobothriidae (Diphyllobothrium dendriticum, D. ditrimum and so on), Tetrabothriidae (Tetrabothrius). They descend from

cestodes - primary hydrobionts, the intermediate and definitive hosts of which were the water animals.

II. The primary atmobionts - the cyclophyllidean cestodes of the land birds, which use the ground or soil invertebrates as intermediate hosts, and sometimes (Paruterina, Cladotaenia and some other species) - the small vertebrates such as the rodents.

III. The secondary amphibionts, such as Fimbriariidae, Ophryocotylidae, Gryporhynchidae, some Dilepididae (Lateriporini, Anomotaeniini) and other of the cyclophyllidean cestodes. Their larvas contaminate the water animals, while adult cestodes contaminate hydrophilous birds.

It is accepted, that the amphibious type of the life cycle of these cestodes is a phenomenon of a primary sequence, phylogenetic research has demonstrated, that their ancestors were the land forms (primary atmobionts). Contemporary hydrophilous birds (such as Laridae, Colymbidae and so on) may have at the same time both primary and secondary amphibionts among the tapeworms.

OBSERVATIONS ON THE DIURNAL RHYTHM OF THE LITTLE AUK
PLAUTUS ALLE L. IN CONTINUOUS DAYLIGHT

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The rhythm of attendance at the colonies and foraging flights of the Little Auk in Spitsbergen was studied during 3 years. Observations showed: (1) the distinct rhythm of activity; (2) the changes of the periodicities, from a period of several days at the prelaying stage to a 24 h period at the chick feeding stage; (3) some independence of the activity rhythm of birds breeding in different subcolonies; (4) the influence of the meteorological conditions on birds activity.

FEEDING ECOLOGY OF THE STARLING (STURNUS V. VULGARIS L.)
IN DIFFERENT HABITATS

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The feeding ecology of the starling (Sturnus v. vulgaris L.) was investigated in summer 1980 in different habitats in the Belgian cherry-growing area during the cherry-period.

Different habitat variables were: grass length, grazing cows and ripening cherries.

Marked differences occurred between food searching behaviour and food intake in different habitats.

There also were strong differences between adults, and first- and second-brood juveniles.

The data are presented and discussed in relation to theoretical optimal foraging models and to literature data concerning the feeding behaviour of the starling.

## GEMMOPHAGIA AMONG EUROPEAN PASSERIFORMES

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Feeding on winter buds of 30 species of trees and shrubs by birds from the families of Sturnidae, Paridae, Sittidae, Turdidae, Ploceidae, Fringillidae and Emberizidae was studied. The kind of plant bud was analyzed in 18 species of birds and the quantity of birds in 14 species.

The birds were found to feed on buds of European cone-bearing trees and shrubs, except Taxus baccata, and on all leafy phanerophytes, except Vaccinium vitis-idea. Some marked preferences were, however, noted for various plants. In the food of the Fringillidae, buds constitute essential calorie providing components. The amounts of buds eaten by these birds during experimental starvation may increase two- to fourfold. Gemmophagia is therefore a means of homeostatic adaptation to food shortage in periods of scarcity.

For insectivorous birds wintering in central Europe, the inside of buds may be a source of vitamins and other biologically active substances.

The amount of winter buds ingested by birds was found to increase considerably between autumn and spring.

Observation on Carduelis chloris showed that female birds eat somewhat larger amounts of winter buds than males. Young greenfinches feed more intensely on winter buds than do adult birds, which feed more on last-year's sprouts.

The proportion of plants preferred by birds in the biocenosis may influence the composition of the winter avifauna of woods and shrub areas.

## EIN BEITRAG ZUR POPULATIONSÖKOLOGIE VON MILVUS MILVUS (L., 1758) UND BUTEO BUTEO (L., 1758) IN DER DDR

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Im 1300 ha großen Laubmischwald Hakel am Rande der Magdeburger Börde, im Nordharzvorland der DDR, wurden zwischen 1957 und 1967 sowie seit 1978 populationsökologische Untersuchungen an den dort siedelnden Greifvogelarten durchgeführt. Im Vergleich der beiden Untersuchungsperioden zeichnet sich für den Rotmilan (Milvus milvus) ein eindeutig positiver, für den Mäusebussard (Buteo buteo) ein leicht negativer Populationstrend ab. Für den Rotmilan ist dies besonders bemerkenswert, da die Hauptbeutetiere Feldhase (Lepus europaeus) und Feldhamster (Cricetus cricetus) einen rapiden Populationsschwund verzeichnen.

Zwischen 1957 und 1967 wurden im Hakel 749 Rotmilane und 282 Mäusebussarde als nestjunge Vögel beringt. Die Wiederfundquote beträgt für die beiden Arten bis Ende 1981 18.2 bzw. 16%. Die Wiederfunddaten werden in Lebenstafeln aufgerechnet. Die Rotmilan-Wiederfunde entfallen auf 9 Länder, 71% von ihnen waren in Frankreich und auf der Iberischen Halbinsel vorwiegend durch Abschuß oder Fang zu verzeichnen. Dagegen spielt der Abschuß von Mäusebussarden aus der Hakelpopulation infolge des geringeren Migrationsverhaltens in die genannten Länder eine weitgehend untergeordnete Rolle. Ein umfassender Greifvogelschutz in Westeuropa würde sich positiv auf die in

vielen Ländern rückläufigen Bestände auswirken.

Die zwischen 1957 und 1967 geborenen Rotmilane aus dem Hakel erreichten eine mittlere Lebenserwartung von nur $2^1/4$ Jahren, dagegen betrug diese beim Mäusebussard 4 Jahre. Die Hauptverluste der Rotmilane sind auf dem Herbstzug, jene der Mäusebussarde in der Winter- und Nachwinterperiode zu registrieren. Es wird darauf verwiesen, daß die Feldmaus-Massenvermehrung (Microtus arvalis) des Jahres 1978 möglicherweise erst 1981 einen phasenverschobenen Anstieg der Brutdichte des Mäusebussards bewirkte, was für ein Erreichen der Geschlechtsreife mit 3 Jahren bei einem größeren Anteil der Jungbussarde sprechen könnte.

HISTORICAL CONCEPT OF THE EUROPEAN AVIFAUNA
ORIGIN AND STRUCTURE
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The complexes of recent avian species, constituting the present avifauna, are conventionally divided into some variously constructed groups, termed as the "faunistic types" (Štegmann, 1938), or some classes of the same "types of distribution" (Voous, 1960). The theoretical basis of this concept are built nearly exclusively on the present distribution of the avian species. Content of a historical aspect in the presented schemes is nearly always negligible.

Climatic and/or ecological changes during the Quaternary are accepted as decisive factors for the origin and development of the present European avifauna. But it is necessary to inquire further back into the earth's history for the origin of nearly all elements of this avifauna. Analysis of the fossil and recent avifaunas indicate, that the European avifauna arose and developed in three waves of the evolutionary radiations.

1) Mesozoic radiation: Nearly no information is known from Europe, but some taxa may persist to the present (Gaviidae, Procellariidae etc.).

2) Paleogene radiation (from Paleocene to Miocene): The North American and European avifaunas were very similar (contrary to the different Asiatic avifauna), consisted of the related ancient forms, limited now mostly to the South America and Old World tropics, but some taxa persist also in the European avifauna (Phoenicopteridae, Gruidae etc.).

3) Neogene radiation (from Miocene to Recent): The ancient European forms spread through climatic changes and through food competition with some more advanced avian species which appeared as immigrants from the subtropics of Asia after the Tethys regression. They form a major part of the present avifauna of Europe. During the Neogene, a passeriform radiation also started.

The Quaternary changes had a character of the repeated emmigrations and reimmigrations of the same groups rather than extinction of the old avifauna and formation of a new avifauna.

AN ATTEMPT OF THE JOINT RESEARCH ON THE BIOLOGY OF THE
BLACK HEADED GULLS BY ORNITHOLOGISTS OF JAPAN AND USSR

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The breeding colony of the black headed gulls Larus ridibundus at the reserve around Lake Klamovsky in the delta of Avacha river, Kamchatka, was observed. The number of breeding pairs of this colony was only several tens in 1967 and increased into several thousands in 1980.

Many gulls lay eggs through June, and first fledglings are seen in the middle of July. Gulls leave the colony in August, and migrate southward in September and October.

Only since the 1973-1974 winter, many black headed gulls have appeared in winter in Kyoto, Japan. From November to April they spend daytime hours on rivers in Kyoto and go over mountains to roost in Lake Biwa. Recently the gulls also expand their wintering areas in many places in Japan.

In the Klamovsky colony, 4100 juvenile gulls have been banded since 1973, including 2600 in 1980. Many banded gulls are recovered widely in Japan, so a great part of gulls from this colony are thought to winter in Japan.

In 1980-1981 winter, about two percent of wintering juvenile gulls in Kyoto had rings which can be judged as the Klamovsky colony members. In Kyoto, gulls were also banded, and their return records show their strong homing tendency to the same wintering area.


REPRODUCTION CHARACTERISTICS OF THE STARLING (STURNUS
VULGARIS) IN NESTBOXES IN BELGIUM (1976-1981)

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Since 1976, 1250 to 1650 nestboxes were placed each year all over Belgium. During these six years (1976-1981) a grand total of 22.368 chicks were ringed. Different parameters of reproduction are analyzed: dates of the first, replacement and second layings; relative frequency of these layings; numbers of fledged young; favorable and unfavorable biotopes; regional abundance of the species; competition with other species of birds, mammals and insects; predators.


ON "DESERTION PERIOD" IN THE NESTLING LIFE
OF THE PUFFIN (FRATERCULA ARCTICA L.)

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Puffin-parents cease feeding their chicks some days before the latter leave their burrow. This phenomenon acquired the name of a "fasting period" or a "desertion period" (Lockley, 1953; Kartashev, 1960; Myrberget, 1962; Skokova, 1967; Korneyeva, 1967; Tatarinkova, Chemyakin, 1970). However, it has been recently stated (Harris, 1976), that no "desertion period" takes place in the puffin chicks life since some of them continue putting on weight

until their last day in the nest and the adults keep on staying in the colo-
ny after the chick had fledged. Our observations of puffins on the Aynovy
Isles (West Murman) showed, that the majority of adult birds leave their
nesting place simultaniously. Some puffins keep on staying in the colony
after their chicks' fledging until their general take-off whereas others
abandon their half-grown youngs which are to leave the burrow at a certain
developmental stage. Thus the presence and duration of a "fasting period" is,
in the long run, dependent on the time for the beginning of nesting which is,
in its turn, related to either spring conditions or to the colony's geogra-
phic position. Hence - the differences in "fasting" duration reported by va-
rious authors: 7.6 days (6-9) - Lockley, (1953); 8.2 days (5-11) - Myrberget,
(1962); 5.4 days (0-15) - Tatarnikova, Chemyakin, (1970). In the warm spring
of 1967 hatching of the puffin on the Aynovy Isles started on June 29, and
on August 12 they began to fledge, the mean "fasting" duration was 3 days,
the maximum - 7. 28% of nests were already left by chicks while their parents
continued bringing food for them. In cold 1968 hatching of chicks began on
July 10, fledging - on August 19, "fasting period" made up 5.7 days (1-15).
After prolonged "fasting" the chicks departing from the burrows were weak
and often fell prey to big sea gulls or starved to death.

## OSMOREGULATION IN PELAGIC MARINE BIRDS (PROCELLARIIDAE)

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Previous studies on salt gland function generally used captive birds adap-
ted to an artificial salt and water regimen, and species which normally are
found on fresh water. The pelagic shearwaters normally experience more ex-
treme conditions (no access to fresh water), and interspecific differences
in proportions of fish and invertebrates in ther diets place differing de-
mands on salt gland secretion and renal-intestinal excretion. The excretory
responses to standard oral loads of sea water were tested in Manx Shearwaters
(P. puffinus, diet mainly fish) and Cory's Shearwaters (Calonectris diomedea,
diet mainly cephalopods), using freshly caught birds to ensure that their
physiological functions were fully adapted to natural conditions. In Puffi-
nus, NaCl accounted for  98% of salt gland secretion osmolality( 1.63 osm/kg
$H_2O$), which is not exceptionally concentrated compared to other birds (as ex-
pected from its diet). Renal-intestinal excretory fluid was only slightly
hyperosmotic (0.72 osm/kg $H_2O$, typical for marine birds) compared to plasma,
but hyperosmotic compared to seawater (1.03 osm/kg $H_2O$). In response to a
seawater load, Puffinus secreted 80-85% of osmolytes via the salt glands and
the remainder via the renal-intestinal system, with a net gain of free water
equivalent to 20% of the load volume. Results for Calonectris will be report-
ed.

# TERRITORIAL DISTRIBUTION AND BIRD POPULATION DENSITY
# IN NORTH-WEST CAUCASIAN MOUNTAINS

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225 bird species of 15 orders are recorded in the North-Western Caucasus avifauna (within the limits of Caucasian reserve and its bodering zones). 152 among them are nesting, 48 - passing en route, 25-wintering.

The variety of the region's avifauna is due to high geographical mountain belt. 92 bird species are nesting in oak-hornbeam-liana forests belt (from 0 up to 300 m below sea-level), among them 18 (19.6%) are typical only for this belt. Bird population density is 884.4 individuals per 1 $km^2$. Erithacus rubecula, Turdus merula and Fringilla coelebs dominate here in different years. In beech and beech-horn-beam forests (from 700-900 up to 1600 m) 96 species are nesting and 14( 14.6%) species are typical of this belt. The population density is 621.2 individuals per 1 $km^2$. Erithacus rubecula, Turdus merula, Parus ater, Sitta europea and Fringilla coelebs dominate here in different years. Only 5 (6.2%) species out of 81 those nesting are typical for dark coniferous forests (from 1200 up to 1500-2000 m). Bird population density is 680.7 individuals per 1 $km^2$. Among the species which predominate in different years we observe: Troglodytes troglodytes, Erithacus rubecula, Turdus merula and Turdus philomelos, Turdus viscivorus, Acrocephalus palustris, Phylloscopus trochiloides, Parus ater, Fringilla coelebs, Spinus spinus, Loxia curvirostra. Subalpine belt (from 1500-2200 m) is a transitional zone from forest to meadow mountain landscapes. Obviously this determines a very low specificity of its avifauna. 2 species (4.8%) are nesting in the above mentioned belt, and 42 species were registred in all at the nesting place. Bird population is 268.3 individuals per 1 $km^2$. Lyrurus tetrix, Anthus spinoletta and Phylloscopus collybita dominate in different years.

33 bird species are nesting in Alpine belt (from 2200 up to 2500 m) and their population density is 211.9 individuals per 1 $km^2$. 7 species (21.2%) are typical. Anthus spinoletta is the only dominant here. Subnivalny belt is slightly expressed. It includes 8 nesting bird species and none of them is typical for the belt.

Thus, the number of nesting bird species is decreasing with the increasing of locality height above sea-level. Their population density is the highest in the lowest belt-oak-hornbeam-liana forests. Bird species of this belt avifauna are very specific. A bit higher a number of typical nesting species decrease and again it goes up in the Alpine belt. Low mountains area is greatly changed by economic activity of people and is accessible for penetration of plain species. Their presence creates the peculiarity of ornithocomplexes. The avifauna specificity increases in Alpine belt due to the nesting of a number of typical Alpine species.

EFFECT OF DEAFENING OR HYPOGLOSSAL DENERVATION
ON PAIRBOND MAINTENANCE IN DUET-SINGERS
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In songbird species which develop antiphonal duets, the exchange of vocal
signals is considered to play an important role in the maintenance of pair-
bonds. We examined its significance in the duet-singer Cossypha heuglini H.
with two kinds of experiments. In the first, we modified the vocal output of
males by sectioning the left N. hypoglossus in control of the left syrinx;
in the other, we deafened females by removing their cochleas. Both operations
resulted in characteristic alterations of the vocal communication between
mates. In spite of these effects, that will be described in detail, pairbonds
between mates remained nevertheless stable. This was particularly significant
when the subjects were confronted with conspecificis.

TERRITORIALITY OF SOME MONOGAMOUS SPECIES OF
CALIDRIDINAE SANDPIPERS
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Four monogamous calidridinae sandpiper species were studied near Uelen in
Chukotski Peninsula, N.-E.Asia, in the summers of 1978-1980. Two patterns of
territorial systems are found among these species. One of the characteristic
features of the Rock Sandpiper (Calidris ptilocnemis) and the Dunling (C. al-
pina) is their high return rates to the breeding region (75.0 and 73.0% of
all colour-banded birds, respectively) and often to the same territories.
This leads to a high degree of mate fidelity in these species. Their terri-
tories are large ($5.2\pm1.5$ and $2.9\pm0.8$ ha) and males establish them on the
first snow-free patches of tundra and defend them during most of the period
of nesting. Worsening weather conditions before egg-laying may lead to tem-
porary breaking down of the territorial dispersal and as a result to the re-
appearence of small sandpiper flocks. The territorial boundaries change re-
latively little throughout the season. Only the absence of snow-free patches
of tundra can make these sandpipers breed in an area adjacent to the one
occupied by them in the preceding year.
    Only some adult Red-necked Stints (C. ruficollis) and Western Sandpipers
(C. mauri) return to their former breeding sites (21.7 and 10.0%, respecti-
vely). The males of these species defend their fairly small territories
($1.25\pm0.55$ and $0.55\pm0.3$ ha) on relatively large patches of the newly exposed
tundra. Usually several males establish their territories close to each
other and the settlement exists for some days. Later unmated males form
settlements in other places whereas mated birds keep close to one place near
the previously defended male territory. The final breaking down of territo-
ries takes place at the beginning of incubation. In bad weather unmated
males of C. mauri can leave the unfavourable region.
    Both of the sandpiper territorial systems show some features of opportu-
nism and have certain advantages in changeable environments.

FOOD NICHE SEGREGATION IN THE GREAT TIT (PARUS MAJOR),
THE BLUE TIT (P. CAERULEUS), AND THE COLLARED FLYCATCHER
(FICEDULA ALBICOLLIS), IN A HUNGARIAN OAK FOREST

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Three food niche dimensions (prey taxa, prey size, prey functional group)
in three common species of hole nesting passerines were measured over three
consecutive breeding seasons. Food samples were collected from nestlings
with neck collar method.

Total niche breadth increased in the order P. caeruleus, P. major,
F. albicollis. It was the most variable in the Great Tit and the most conser-
vative in the Collared Flycatcher from year to year. Niche breadth was the
greatest in the Collared Flycatcher along the food composition and the prey
functional group while the Great Tit had the most variable prey by size dis-
tribution. Niche overlap between years was the smallest in the Great Tit.
Patterns of dietary overlap (along all three food dimensions) among species
were quite inconsistent from year to year, although the food composition
overlap between the Collared Flycatcher and Blue Tit was consistent.

The food composition seemed to be more important than the other two niche
dimensions in niche segregation of these three species.

DIE BESONDERHEITEN DER FRÜHLINGSMIGRATION DES
ALPEN-STRANDLÄUFERS IM NORDWESTLICHEN SCHWARZMEERGEBIET

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Der Fang und die Beringung dieser Art wurde in der Frühlingszeit in den
Jahren von 1977 bis 1981 im südlichen Teil des Tiliguler Limans durchge-
führt (42 km. östlicher von Odessa). 950 Vögel wurden beringt, unter ihnen
waren 61 Vögel mehrmals in verschiedenen Jahren gefangen worden. Gegen 30%
der Vögel halten sich derselben Zugrichtung auch in den nächsten Jahren.
Anfang April kommen die Alpen-Strandläufer in das Gebiet, das untersucht
wird, geflogen, vorwiegend im Ruhekleide, einzelne Vögel im Stadium der Teil-
mauser. In dieser Periode beginnt die Kleingefiedermauser, die gegen Ende
Mai zu Ende geht. Die Jungvögel mausern sich später. Die Alpen-Strandläufer
besetzen Plätze des Limans mit gutem Nahrungsangebot für lange Zeit, für
etwa 20-38 Tage. Ein besonders langer Aufenthalt ist bei Vögeln festgestellt,
die in der dritten April Dekade beringt worden sind. 50.9% der Vögel gehören
zu den nordöstlichen, 39.1% zu den nordwestlichen und 10% zu den zentralen
Populationen. Die gemauserten Vögel erreichen die maximale Wohlgenährtheit
und von Mitte Mai an bis Anfang Juni beginnen einzelne Schwärme ununter-
brochene Wanderungen zum Brutgebiet.Zu derselber Zeit steigt die Gesamtanzahl
der Art, was vermutlich mit dem Zug verschiedener Populationen, die sich
irgendwo südlicher gemausert haben, verbunden ist.

Im Frühling wurden die Vögel gefangen, die im Herbstzug in Finnland,
Schweden, in der DDR oder auf den Überwinterungsstellen in Frankreich, Tune-
sien beringt worden waren. Die Analyse dieser Tatsache gibt die Möglichkeit,
die Vermutung auszusprechen, daß die Alpen-Strandläufer de·· obengenannten

Populationen zur Überwinterung die nördliche europäische Küste entlang flieg-
en, und über das westliche Schwarzmeergebiet und über das Binnenland des
Kontinents zurückkehren. Davon zeugt der im August bei Gdansk (Polen) ge-
fangene Alpen-Strandläufer, der im Mai desselben Jahres im südlichen Teil
des Tiliguler Limans beringt worden war.

WIEVIELE BRUTPAARE DES WEISSEN STORCHES BRÜTEN ERFOLGLOS?

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Die Zahl der erfolglos brütenden Brutpaare des Weissen Storches schwankt
nach Jahren und Gebieten. Nach verschiedenen Autoren blieb in Oldenburg
(BRD) in 50 Jahren im Mittel 45% der Brutpaare des Weissen Storches ohne
Nachwuchs, in der Umgebung Hamburgs betrug die Zahl solcher nachwuchsloser
Brutpaare in 12 Jahren durchschnittlich 38.2%, in den Niederlanden in 14
Jahren durchschnittlich 33.9%, in Dänemark in 24 Jahren durchschnittlich 32%,
im Gebiet Hannovers in 12 Jahren durchschnittlich 38.2% usw. Diese Vergleichs-
zahlen stammen sämtlich aus dem Gebiet der rapiden Abnahme des Storchbestand-
es. In mehr östlich liegenden Gebieten der Storchverbreitung ist die Zahl der
nachwuchslosen Brutpaare des Weissen Storches jedoch bedeutend geringer: im
Nordteil der DDR beträgt sie 19.5%, 27.6% und 28% in den einzelnen Zähl-
jahren, in Polen 13.4%, 19.0% und 23.4%, in Estland in 27 Jahren durch-
schnittlich 26.4%. Auffallend wenig erfolglose Brutpaare des Weissen Storch-
es zählte man in Ungarn (2% in 1958), Litauen (5.7% in 1974) und Lettland
(3% in 1934 und 4% in 1974). Es ist nicht ausgeschlossen, dass in diesen
Ländern viele mit jungenlosen Brutpaaren besetzte Horste nicht erfasst wur-
den. Diese Angaben lassen den Schluss zu, dass in Estland, wo in 27 Jahren
durchschnittlich 26.4% von den Brutpaaren jungenlos blieb, die Brutpaaren-
zahl sich in dieser Zeitspanne 3.3 mal vergrössern konnte, in Westeuropa bei
mehr als 30% jungenlosen Brutpaaren aber eine allgemeine Abnahme des Bestand-
es eingetreten ist.

DER "ATLAS DER VERBREITUNG PALAEARKTISCHER VÖGEL" -

AUFGABEN UND ZEIL

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Der "Atlas der Verbreitung palaearktischer Vögel" wurde 1957 von Akademie-
mitglied Professor Dr. Erwin Stresemann, Berlin, als tiergeographisches und
ökographisches Kartenwerk gegründet und mit Professor Dr. Leonid A. Portenko,
Leningrad, herausgegeben. Es sollte ursprünglich aus den etwa 800 Brutvogel-
arten der Paläarktis etwa 200, größtenteils den Singvögeln angehörend, aus-
wählen, von deren Kartierung man sich einen besonders großen wissenschaft-
lichen Gewinn versprechen konnte. Verbreitungskarten geben festen Anhalt für
die Rekonstruktion des Vorgangs der Ausbreitung, sind wichtig für Ökologen,
Faunisten, Evolutionsforscher, Taxonomen, Paläographen, ferner bedeutsam für
alle, die sich mit dem Schutz oder der wirtschaftlichen Nutzung freilebend-
der Vögel befassen. Jenes Auswahlprinzip wird beibehalten. In gegenwärtiger

Zeit, da der Rückgang der Artenzahl an Vertebraten weltweit und rapide in Erscheinung tritt,ist unserem "Atlas" als weitere Aufgabe zugefallen, diesen Prozeß anhand markanter und vorzugsweise betroffener großer Vogelformen zu verfolgen und zu dokumentieren. Insofern werden ab Lieferung 7 (1978) zunehmend Non-Passeres bearbeitet, deren einst große Areale - fast immer aus umweltproblematischen Gründen- heute zu kleinen Refugien zusammengeschmolzen sind, z. B. Nipponia nippon, Geronticus eremita, Grus leucogeranus, Grus japonensis, Grus vipio, Grus monacha, Grus nigricollis, Larus relictus. Bis dato sind 10 Atlas-Lieferungen mit 130 Arten erschienen.

Die Verbreitungskarten, Fundortlisten, Literaturlisten und Begleittexte (Kriterien: Subspezifische Gliederung, Verbreitung, Ökologie, Wanderungen) werden von Mitarbeitern der Akademie-Forschungsstelle für Wirbeltierforschung in Berlin (DDR) und des Zoologischen Instituts der Akademie der Wissenschaften der UdSSR in Leningrad gemeinsam erarbeitet. Als Herausgeber fungieren Professor Dr. Dr.Heinrich Dathe, Berlin, und Dr. Irena A. Neufeld, Leningrad.

LONG-TERM STUDY OF POPULATION DEMOGRAPHY OF THE
BLACK-HEADED GULL (LARUS RIDIBUNDUS L.) IN LATVIA
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Different aspects of the demography of generally increasing population of the Latvian Black-headed Gull (1944 - 10000, 1979 - 97000 pairs) were studied since 1962, mainly on Lake Engure (1949 - 200, 1972 - 26000, 1980 - 20000 pairs). Mass-scale trapping of adults on nests, analysis of random recoveries as well as productivity studies applying the method of fenced areas are used.

Mortality of chicks up to the 25th day of life (data of 1974-1981) averaged 42.9% (in separate years 33.6-54.3%). On the average 60.5% of lost chicks died by the 4th day of life and about 80% - by the 10th day. Number of fledged young per pair decreased from 1.55 in 1974 to 0.94 in 1981 (average - 1.19).

Mortality in the first year of life after fledging is 38%, and 15% in the following years.

Distribution (per cent) of birds nesting for the first time in their life for females is: 1 year old - 5%; 2 - 64%; 3 - 31%; and for males: 2 year old - 40%; 3 - 49%; 4 - 11%. This distribution is likely to change according to the density of population.

With 1.55 young fledging per pair (1974) and other indices as mentioned above, the population would have the growth rate observed on the Lake Engure in 1950s-1960s, if the immigration and emigration are approximately equal.

## FEEDING FLIGHTS OF THE BLACK-HEADED GULL
## LARUS RIDIBUNDUS L.

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Feeding places of the Black-headed Gull of Lake Engure (west coast of the Gulf of Riga in the Baltic, 35.4 sq. km, 26000 nesting pairs in 1972, about 20000 in 1980) changed during the last decade and the distances of feeding flights increased probably due to decreasing possibilities to get anthropogenic food near the lake.

Feeding flights have been studied in 1980-1981 by means of trapping and painting (picric acid) birds in feeding places (fish-canneries, mink farm) located 3-70 km away from the breeding colonies. Painted birds were recorded visually both on the lake and outside it. Totally 4085 birds were painted; number of sight records of them on the lake and outside it were no less than 330 and 180, respectively.

Feeding flights at distances up to 70 km from the breeding colonies are proved, and gulls flow regularly in big numbers up to 40 km. Feeding territories of the Engure gulls and those nesting of Lake Kanieris (35 km apart, about 5000 breeding pairs) overlap considerably.

There are no colony-specific feeding places during the whole breeding season, although birds nesting in the northern and southern half preferred to feed north and south of the lake, correspondingly. These differences were more pronounced in 1981.


## BIRDS IN THE FOREST ECOSYSTEMS DESTROYED BY
## HERBICIDES IN SOUTH VIET-NAM

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The US carried out a massive herbicidal programme during the Second Indochina war. It was aimed, for the most part, at the forest of South Viet-Nam. Herbicidal attack has a serious impact not only on the autotrophic component of this ecosystems, but on the higher level, heterotrophic ones as well, among birds.

District A-luoi, a typical humid forest was sprayed many times from 1965 to 1969. All vegetation cover was destroyed and has not been reestablished. The decimation of the vegetation brought about the long-term changes in the biotic community. In the past, the fauna of birds was very rich (about 150 species), but today, only 18 species are found. The use of herbicides may have placed in jeopardy the actual survival of some endangered endemic species.

An estimated 125000 ha of true mangrove along the southern coast of Viet-Nam was subjected to military herbicide spraying. Virtually noting remained alive after a single herbicidal attack. More than 50 breeding species of birds were found in the avifauna. They formed a number of special communities called "birds' field". After chemical attack they were destroyed and now several new ones have been reestablished. Two formally abundant species are entirely absent and many others have become rare.

THE VARIABILITY OF LAGOPUS LAGOPUS CLUTCH SIZE
IN THE NORTH-EAST TUNDRAS OF THE EUROPEAN PART OF THE USSR

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In Bolshezemelskaya tundra and on the Jugorsky peninsula 160 finished
clutches with eggs from 3·to 12 were inspected. Clutches of 8 (22.5%) and 7
(17.5%) prevailed and nests with minimum (3-4) and maximum (11-12) eggs made
accordingly 5.5. and 3.7%. During 11 years the middle laying size oscillated
within the limits of $6.09 \pm 0.39$ (n=22, 1970) and $8.48 \pm 0.47$ (n=27, 1980). The
extreme laying limits were modified too. In the years of high number and
active participation of one-year-old individuals in the reproduction process
the modification of egg reaches 28-29,5. In the years when mainly two-year-
olds and older Lagopus were reproducting, the variability of the laying size
went down to 10-12%. Annual deviations from the middle of many years laying
size (7.7 eggs) are insignificant, and only twice they reached 21-22%. The
analysis of dependence of middle size laying on meteoconditions (35 parame-
ters were taken) didn't show any kind of connection with most of them: corre-
lation was observed only with the sum of temperatures in the last decade of
May (r=0.672) and the number of precipitations in June (r=0.554).

CACHING AND RECOVERY OF FOOD BY ROCKS AND CARRION
CROWS: RELATIVE CONTRIBUTION TO THE WINTER DIET

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Rooks (Corvus frugilegus) and carrion crows (C. corone) were observed to
cache acorns (fruit of Quercus robur) during autumn, and invertebrates (ma-
inly large earthworms, Lumbricidae) throughout the year. Artificial food-
stuffs (mainly bread) were also hidden. Rooks cached acorns at a time of
relative food abundance. Rooks and carrion crows cached invertebrates on
days when their intake rates of invertebrate prey were higher than the mean
for that season. Recovery of acorns occurred on days when intake rates of
other prey were lower than the mean for that season. In periods of prolonged
frozen soils, and in late winter when stubble grain was depleted, recovery
of cached acorns provided higher intake rates of calories, and comparable
rates of protein-containing material, compared to other available prey. Reco-
very of invertebrate caches was not proven conclusively to occur. The rela-
tive value of recovering other cached items could also not be quantified.
Recovery of some items gave evidence of exact-location memory, but recovery
of acorns indicated only memory of the general area in which caches had been
made. It is concluded that acorns, cached by rooks (and perhaps crows) at a
low cost, could prove important as an "insurance" source of high-energy food
during periods of temporarily-reduced availability of normal winter prey.

POLYGYNY IN THREE PASSERINE SPECIES FROM THE PRIMAEVAL
FOREST OF BIALOWIEZA

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During 4-yr study carried out in Bialowieza National Park (NE Poland) re-
gular occurrence of polygyny in Phylloscopus sibilatrix, Phylloscopus colly-
bita and Troglodytes troglodytes was recorded.

As a rule the polygynous males were paired simultaneously only to two
females, trigamy was exceptional.

The polygynous birds were recorded almost exclusively in optimal habitats.

Production of young per female in polygynous groups was not smaller than
production of young by females mated to monogamous males.


THE DISTRIBUTION AND NUMBER OF THE MUTE SWAN IN POLAND

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Analyzing the data provided in questionnaires it has been estimated that
during the period 1978 and 1979 about 2500 prs of the mute swan nested in
1500 localities. Only a few bodies of water had larger concentrations of
breeding birds.

With an increase in the number of new localities and the range expansion
of this species to the south, many of the large breeding concentrations which
were known during the period 1930-1960 disapeared.

Mute swans breed over almost the whole of Poland except in the piedmont
area, especially in the south-eastern part of the country. Their density
shows a large variation and fluctuates from 25 to 0.1 prs/1000 $km^2$. The high-
est density is found in Gorzów and Bydgoszcz areas (voivodships). The north-
ern and northeastern parts of Poland are the areas of high density of mute
swans, about 10-20 prs/1000 $km^2$.

It appears that the Masurian lakes are almost fully saturated with breed-
ing birds and a strong expansion has been recorded on new reservoirs in the
western and southern parts of Poland. During the 40 years 10-fold increase in
the number of nesting mute swans occurred in areas west of the Vistula and
only a 50% increase in the area east of the Vistula.


SEXUAL SIZE-DIMORPHISM IN THE GROWTH OF MACRONECTES
PETREL CHICKS

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Sex had a marked effect upon the development of chicks of Northern and
Southern Giant Petrels, Macronectes halli and M. giganteus respectively,
during studies of development from hatching to fledging during two breeding
seasons at Subantarctic Marion Island (46S; 37E).

Chicks could be sexed by a clear bimodality in the rativ between culmen
length and tarsus length at an age of 105 days. In both species, more female

chicks existed than male chicks. Sex of the hatchling was uncorrelated to fresh egg weight. Significant sexual differences in culmen length existed in each species at hatching and throughout the chick-rearing period.

Significant sexual differences in body weight and in tarsus and manus length developed in giganteus soon after hatching but only later in halli. Male halli chicks fledges significantly later than female chicks but there was no sexual difference in the fledging time of giganteus chicks. In both species male chicks received heavier meals than female chicks but in giganteus male chicks also received significantly more meals than females.

## DISPERSION OF CARRION CROWS CORVUS C. CORONE DURING THEIR FIRST YEARS OF LIFE UP TO TERRITORY FORMATION

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Near Brunswick (FRG) we are carrying out a long-term study of a crow population of about 60-80 breeding pairs. Since 1971, the nestlings are marked with plastic wing-tags for field identification.

1.1. Shortly after fledging, losses of young seem to be considerable.

1.2. Some weeks after fledging, part of the young leave their birthplace either alone or with their parents.

1.3. A considerable number of birds stay near their birthplace whereby the family bond may continue.

1.4. Of those mentioned under (1.3.), some additional birds leave the area at the beginning of the next breeding season when their parents and other territory owners become more and more aggressive.

Dispersion of young birds is as follows:

2.1. The dispersing birds spread in all directions up to about 70 km from their birthplace.

2.2. The birds still near their birthplace at the end of their first year of life show a strong tendency to stay there until establishing a territory (Geburtsortstreue).

3.1. After leaving their parents, the young birds join a flock of non-breeding birds of various ages during the breeding season.

3.2. Pair-formation seems to take place in the flock and when the birds are 2-3 years old, they leave the flock to establish their own territory.

## SETTLING AND START OF REPRODUCTION AS A SEVERAL YEARS PROCESS IN CARRION CROWS CORVUS C. CORONE AT HIGH POPULATION DENSITY

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The habitat of the crow population studied in N. of the country by means of wing-tagging of nestlings (see other poster paper of the authors) consists of high-intensity farmland with several small woods. The population is stable on a high-density level with only little disturbance by man. Nearly all suitable sites are occupied by pairs, mostly holding their territories throughout the year. Moreover there are flocks of non-breeding birds of

various ages. The pairs establish territories when 2-4 years old, but most
are unfavourable, some lacking any nest-site. The following years, the birds
seek to improve their territory by moving its borders or taking over a near-
by territory.

The activities of the birds as far as they were paired and territorial
are:

2-year-old: partly nest-building, only one case of breeding.
3-year-old: some without any nesting activities, about half the remaining
            majority building only a nest and half breeding.
4-year-old: mostly breeding, but some recently settled pairs only build a
            nest or do not even do that.
5-year-old: nearly all birds breeding.

Reproductive rate in the first years of breeding is very low but rises
later. The gradual development of reproductive activities is considered a
consequence of high population density operating mainly through territorial
behaviour, thus proving part of a self-regulating mechanism.

SOME ECOLOGO-MORPHOLOGICAL PECULIARITIES OF THE
JAW APPARATUS IN LARKS (ALAUDIDAE)
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The larks show a wide rangs of bill shapes - from the weak beak in Lullu-
la and Alauda to the thick coniform one in Melanocorypha and Rhamphocorys.
This variation in bill size and shape is reflected in the differences observ-
ed in the unusual internal morphology of the jaw apparatus of this family.
The morphological pattern of the lark jaw apparatus is also known from lite-
rature on the gallinaceous birds. It includes features such as the aberrant
quadrate-mandibular joint structure and the false zygomatic arch (ossified
aponeurosis of the M. adductor mandibulae externus medialis fused with the
postorbital process). These features are considered to form part of adapta-
tion for tearing off flat pieces of food. Additional information about the
diet and feeding habits of larks suggests detail adaptations in this group
which are parallel to those in the fowls based on the different original con-
ditions in the two groups.

ENERGETIC CONSTRAINTS OF CLUTCH SIZE AND TIME OF
BREEDING IN TEMPERATE ZONE BIRDS
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The timing of breeding and clutch size of birds have been extensively dis-
cussed in the literature. We produced a comprehensive model, using the great
tit in Oxford as a subject, which integrates climatological, physiological
and ecological data.

The following factors have been incorporated in the model: (1) day length
during the breeding season (i.e., available foraging hours); (2) daily and
seasonal fluctuations in ambient temperatures and their effect on (a) nest

1192

box temperature; (b) female's metabolic rate (during night and day); (c) attentiveness at the nest; (3) cost of egg formation; (4) clutch size; (5) cost of brooding the chicks; (6) energy requirements of the chicks; (7) feeding of the female and chicks by the male; (8) energy reserves of the female; (9) availability of food.

The results of the model are in good agreement with many of the observations made in nature and explain fully the following negative correlations: (1) brood size (above mean brood size) and chick weight; (2) mean ambient temperatures prior to laying and laying date; (3) breeding density and clutch size; (4) brood size and time interval between successive clutches. It also fully explains the north-south decrease in clutch size in great tit, and partially the following field observations: (1) the larger clutches of early breeders; (2) the early breeding of hole nesting birds; (3) the late laying in some polygamous species.

Simple field experiments are suggested to test some of the assumptions and predictions of the model.


FLUCTUATIONS IN THE GROUPSIZE OF THE WHITEHEADED
BABBLER TURDOIDES AFFINIS
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The population size of the Whiteheaded Babbler Turdoides affinis and the patterns of changes in numbers undergone by its groups were studied in a $2.27 \ km^2$ tropical dry secondary scrub in Calicut, South India, for a period of four years from September 1973. The Whiteheaded Babbler lives in groups of 3-14 birds in the study area. The size of a particular group seems to vary within fairly narrow limits. Over 4 years most groups varied up to twice their minimum size. This suggests that factors influencing group size tend to adjust quite rapidly.

The groups of Turdoides affinis living in the residential areas were larger and had a larger rate of increase. In most cases the group size was between 4 and 8 and only four groups reached the maximum size of 14. None of the groups contained 14 members for longer than 8 months and after reaching this size all of them underwent a reduction in size. The groups with 10 or less birds were more persistent. Intergroup movements of all age classes were noticed frequently in Turdoides affinis. These movements help to regulate the group size, increase interbreeding between unrelated birds, and improve the chances of a low ranking bird to breed in another group.

The Whiteheaded Babbler breeds throughout the year, and the overall breeding season of the species is probably the longest of any passerine bird found in the study area. The average nesting success of 4 years was 41.6%. On the whole the overall tendency was increase in population numbers.

BIRD MIGRATION AND WEATHER IN SOUTH-EASTERN PART
OF THE BALTIC REGION

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In 1974-1977 radio-location studies on bird migration were carried out
day and night in the continental part of Lithuania and on the coast of the
Baltic sea. 8 processes of the intensity of diurnal and nocturnal, spring
and autumn migration were compared with 20 meteorological and synoptical pa-
rameters of weather using factor analysis and stepwise multiple linear re-
gression. The main parameters influencing the intensity of flight in spring
(registered by the radar) were cloud type and weather temperature, while in
autumn the flight was dependent on cloud type and wind direction. One or
another weather parameter influencing migratory intensity was significant as
far as that parameter caused unfavourable conditions for bird flight.


ADAPTIVE BEHAVIOURAL MECHANISMS OF THE CORVIDAE SPECIES

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As is known, there are birds in the Corvidae species which have a very
high organization of the brain. Their brain is relatively large and has a
fine differentiation of the micro and macro-structures. In natural environ-
ment the behavior of Corvidae birds is characterized by high adaptivity and
individual peculiarities. It has been shown that their manipulatory - in-
vestigating activity is variable and changeable both in its form and inten-
sity. It is supposed that this developed manipulatory - investigating acti-
vity is an essential part of instrumental activity which was observed in the
Cordivae in natural and experimental conditions.

The study of the Corvidae ability to operate with the empirical dimensi-
ons of objects has proved that they are quite capable of solving this task
and in this indication of their reasoning ability they are very close to
carnivorous mammals such as bears, dolphins and monkeys (Krushinsky, Zorina,
Dashevsky, 1979, 1980). We used also a new more complicated test, previously
applied only for probing human mentality. In this test the birds had to re-
veal the algorythm of change in the food bait position, when the algorythm
was determined by the experimentator. Our data showed that several individu-
als among the observed birds solved the test and their performance was quite
comparable to that of young children.

Our data prove the existence of Corvidae's high level of reasoning acti-
vity and allows a conclusion that their advanced behavioral adaptivity in
natural habitats is partly due to this ability.


SPACE RELATIONS IN SOME BIRD SPECIES IN THE
CAUCASIAN REGION

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The Caucasus is that part of Palearctic where very particular space rela-
tions among taxomically close bird species occur. Buteo buteo is an example

of secondary integration of conspecific, though divergent enough, forms. Relations typical of the subspecies notion are characteristic for Phylloscopus collybitus and Ph. lorenzii. Besides, a member of markedly different races - isolationists of some widely-spread species (Saxicola torquata armenica) dwell here. These and some other situations connected with distribution and taxonomic relations of birds in the above-mentioned retion are very good models for research on allopatric speoies formation and space isolation of populations.

BIOLOGICAL BASIC FEATURES OF TIME CODING OF
ACOUSTIC INFORMATION IN BIRDS
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The transmission of acoustic information using time coding is clearly displayed at early stages of bird vocalization. The analysis of sound signals of embrions and ohicks of different orders showed that the physical structure of these signals is identical for all orders, but the rhythm pattern is dependent on lung breath. Any alarm situation or a sense of hunger cause more frequent breathing, leading to shorter time intervals between individual calls. This is an important mechanism in the transmission of situational changes in behaviour by an acoustic channel. The use of time coding of acoustic information is charaoteristic of adult birds too. The analysis of marital signals of close bird species shows that time variations are the basis for the acoustic isolating mechanism.The prinoiples of time coding are respo nsible for individual recognition inside the species.This becomes quite obvious when the method of "sound trap" is applied. The breach in acoustic recognition is shown by the denervation of the sirinx in one of the mating pairs. When this technique is applied the time structure of the song is changed, while the frequency spectrum remains the same. Birds' extensive use of time coding acoustic information is determined by the work of the birds' acoustic analizer. Fine analysis of time coding in sound signals is already distinguishable on the cochlea and on primary hearing nuclei.

EARTH'S MAGNETISM AND THE SUNSET ORIENTATION OF HAND-
REARED AND WILD MIGRATORY SPARROWS
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Recent studies have suggested that nocturnal migrants can use the position of the setting sun as an independent orientation stimulus. None of these studies, however, controlled for directional information, gained from earth's magnetism. I examined the importance of directional information from magnetism on the sunset orientation of hand-reared and wild Savannah Sparrows (Passerculus sandwichensis). During spring migration, 1981, six hand-reared and six wild birds were tested for their sunset orientation on alternate days in the normal earth's magnetic field and a magnetic field with a null horizon-

tal component. Tests began when the disk of the sun fell below the horizon and ended when Polaris became visible. The handreared birds oriented north-west when tested in the normal earth's field. The hand-reared birds were randomly oriented in the null field. Directional information from magnetism was necessary of hand-reared birds without prior migratory experience were to orient at sunset. The wild birds oriented northwest when tested in the normal earth's field. The wild birds were bimodally oriented along a north-west-southeast axis when tested in the null field. The two wild bird distri-butions, however, did not differ statistically. Wild birds with prior migra-tory experience could use sunset position as an independent orientation sti-mulus, but information from magnetism may be important for these birds as well in a way not yet determined.

MIGRATORY ACTIVITIES OF SOME EMBERIZA SPECIES EXPOSED
TO DIFFERENT ARTIFICIAL LIGHTS AND TEMPERATURES

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The migratory activities in cages of Emberiza rustica and E. schoeniolus have been studied in comparison with those of non-migratory Passer m. satu-ratus.

The first experiment was conducted by placing the above-named species in three chambers at different artificial temperatures 23°C, 15°C and 8°C, res-pectively. The period of light increased gradually from 9 to 15 hours then decreased from 15 to 9 hours.

In E. rustica, all the three different temperatures induced the onset of Zugunruhe in spring, whereas Zugunruhe was induced again only at the low tem-perature, 8°C in autumn. In E. schoeniolus, the onset of Zugunruhe was indu-ced at the favorable temperature, 23°C, only in spring, whereas the Zugun-ruhe has not been observed at the low temperature, 8°C. On the other hand, in P. m.saturatus, on Zugunruhe was found in the three bird groups through-out the experiment.

The second experiment was conducted by placing E. rustica in three cham-bers equipped with three different artificial lights, 16L, 12, and 8L. The temperature increased gradually from 8°C to 22°C then decreased from 22°C to 8°C.

The results from the second experiment show that the increased Zugunruhe appeared in the temperatures between 14°C and 18°C.

# POSTER PRESENTATIONS

P.N. BECKER

COMMON TERN BREEDING SUCCESS AND NESTING ECOLOGY UNDER PREDATION PRESSURE OF HERRING GULLS

P.N. BECKER, M. ERDELEN

DISTRIBUTION OF HERRING GULL EGG SIZE AND NEST DENSITY IN THE MELLUM-COLONY IN RELATION TO VEGETATION HEIGHT

I.N. DOBRYNINA

CHARACTERISTICS OF SOME BIRD SPECIES MIGRATIONS ACCORDING TO THE RINGING DATA

V.M. GAVRILOV

ENERGY OF EXISTENCE AT 0° AND 30° BASAL METABOLISM OF INSECTIVOROUS AND GRANIVOROUS PASSERIFORMES: THEIR SEASONAL CHANGE AND DEPENDENCE ON BODY MASS

S.P. KHARITONOV

ON STRUCTURE OF BLACK-HEADED GULLS (LARUS RIDIBUNDUS) COLONIES

O.L. SILAJEWA

SOUND IMITATION IN THE FORMATION OF COMMUNICATION BETWEEN MAN AND BIRDS

S.M. SMIRENSKY, A.L. MISHCHENKO

TAXONOMIC STATUS AND HISTORICAL FORMATION OF THE AREA OF COMMON SWALLOWS (HIRUNDO RUSTICA) IN THE AMUR REGION

L.S. STEPANYAN

THE GEOGRAPHICAL CORRELATION OF MORPHISM PHENOMENA IN BIRDS IN CENTRAL ASIA

V.A. ZUBAKIN

TYPES OF COLONIALITY IN THE FAMILY LARIDAE

COMMON TERN BREEDING SUCCESS AND NESTING ECOLOGY
UNDER PREDATION PRESSURE OF HERRING GULLS

Peter H. Becker

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STUDY AREA AND METHODS

Subject of this study is a Common Tern colony on Mellum (1979: 80, 1980: 125, 1981: 160 pairs) adjacent to a Herring Gull colony of about 10,500 pairs. During checks every 2 days (1979: 4 days) nests, eggs and chicks were marked and recorded until the end of the breeding period (end of July)(Figs.1, 2).Chicks of ≥ 18 days were counted as fledged (1979: ≥ 14 days). By cartography of nests we measured the nest density (number of nests in $r ≤ 5$ m around each nest; only nests having taken part in ≥ 50% of the reference nest's breeding time). In 1981 the colony area was fenced with chicken wire (height of about 30 cm). Results mainly refer to early nests (pentade 28-34). In addition in 1979 and 1980 we observed the colony during 72 h resp. 144 h from a hide (half the hours spent on incubation, and half on time after hatching)(Table 1,2).

T a b l e 1. Age groups, death causes and survival of chicks in 1980

| Age group Chicks | 1-5 (n = 248) | 6-10 (n = 128) | 11-15 (n = 84) | 16-17 (n = 55) | 18 (n = 51) |
|---|---|---|---|---|---|
| dead (n = 90) | 65 | 16 | 7 | 1 | 1 |
| % dead | 72.2 | 17.8 | 7.8 | 1.1 | 1.1. |
| % chicks | 26.2 | 12.5 | 8.3 | 1.8 | 1.9 |
| disappeared (n=108) | 55 | 28 | 22 | 3 | ? |
| % disappeared | 50.9 | 25.9 | 20.4 | 2.8 | |
| % chicks | 22.1 | 21.8 | 26.1 | 5.4 | |

T a b l e  2. Number of chicks disappeared compared with observed chick predation in 1980

| observation period | number of chicks disappeared | watched cases of chick predation ($9^h$/day, x 2; () = including cases with uncertain result) |
|---|---|---|
| 21.-24.6 | 18 | 14 (20) |
| 29.6.-2.7 | 27 | 26 (48) |

RESULTS

1. Egg loss increased with laying time (Fig. 3, Table 3). Eggs of late nests were robbed by an Oystercatcher (Haematopus ostralegus).

2. Breeding and fledging success is negatively correlated with the pentades of egg laying  Table 3). Only nests started during the first 4 pentades (1980: 3) achieved fledged chicks.

3. This was mainly caused by an increasing chick loss with advancing breeding time. The investigation of chick fate had the following results:

a)More than 70% of the dead chicks and more than 50% of the chicks having
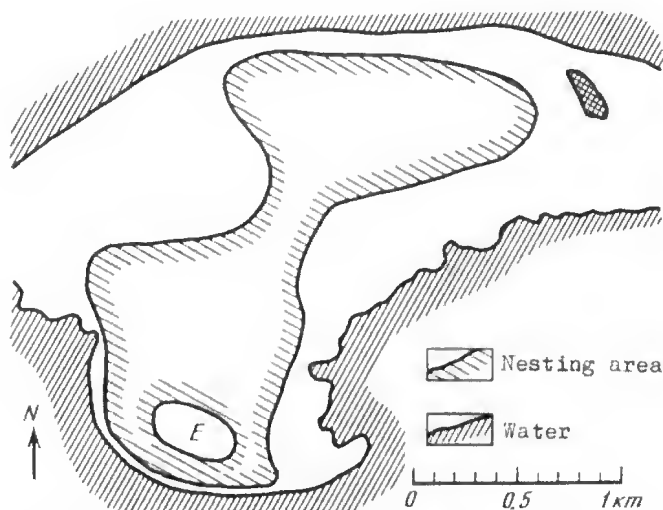
F i g. 1. The Common Tern colony (black) on Mellum next to the Herring
Gull breeding area (hatched)



F i g . 2. Age groups, death causes and survival of chicks in 1980
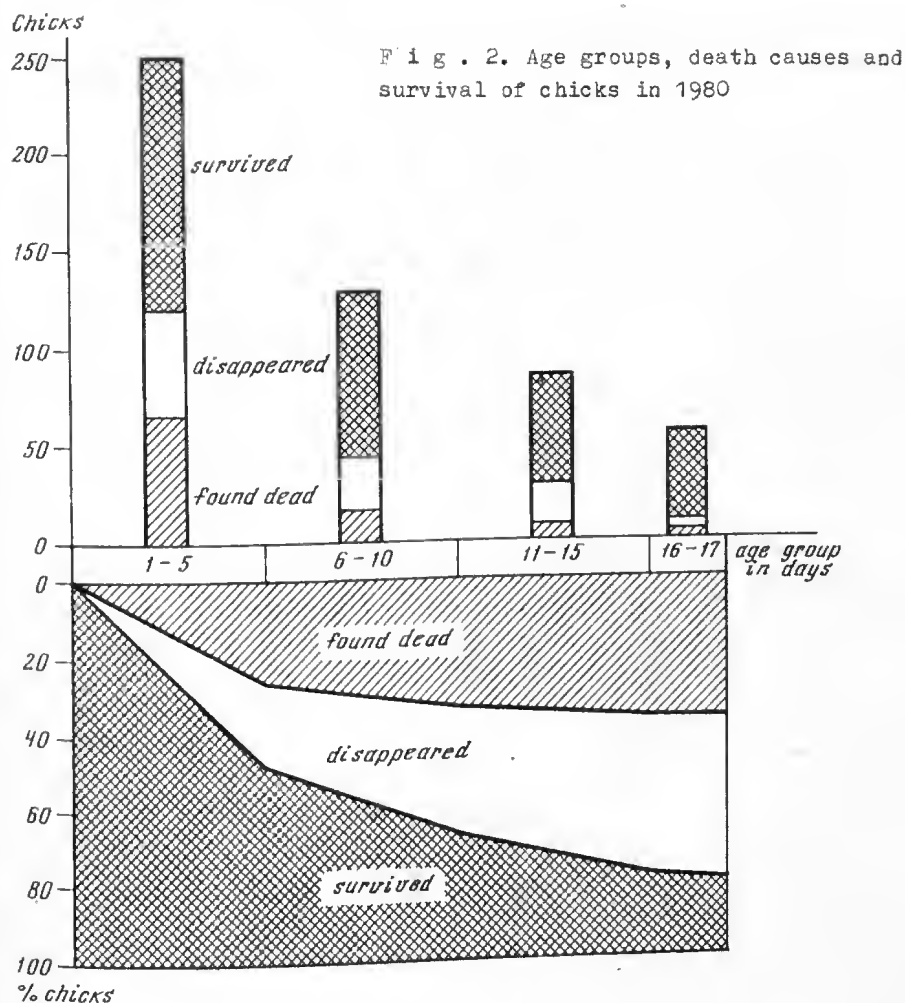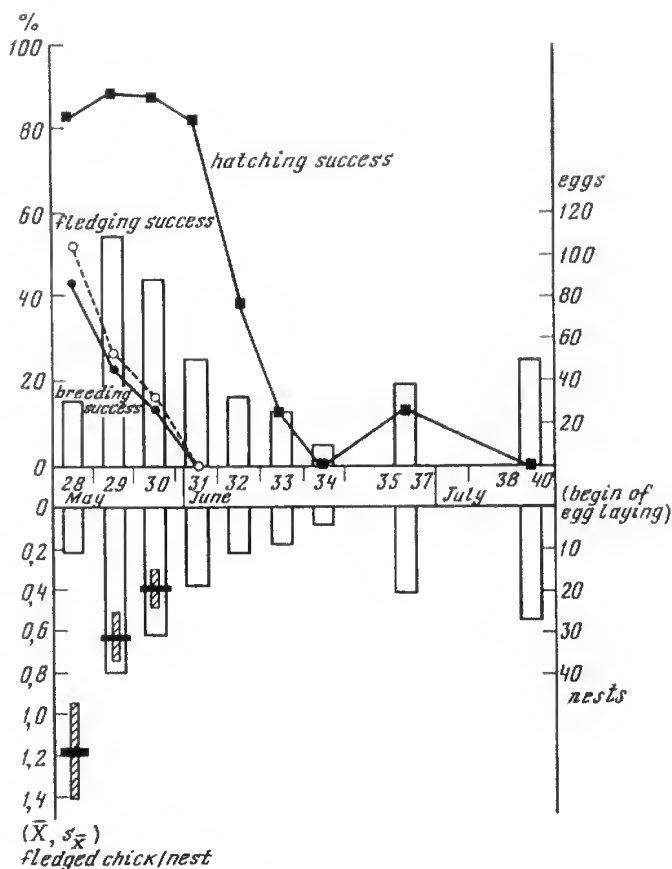
F i g. 3. Breeding success in relation to time of egg laying in
1980 (columns: eggs resp. nests)

disappeared were 1-5 days old (Fig. 2, Table 1). Most dead chicks were found
after peak of hatching.    Disappearance was the main cause of chick
loss in each of the 3 years (Table 3).

b) Refering to 1980:    After hatching of about 1/4 of chicks (c.60),
the number of disappeared chicks increased constantly up to a maximum of
about 11 chicks/day; Thereafter - again at about 60 chicks alive - the dis-
appearance rate decreased rapidly (also in 1979 and 1981,).

4. Besides Larus ridibundus (2 cases) in 1980 we mainly observed Herring
Gulls robbing chicks (29 attempts, at least 19 successful; in 1979: 5, at
least 1 successful). Watched chick predation changed according to the course
of disappearance (Fig. 5), and the numbers of chicks disappeared and robbed
corresponded during the observation time (Table 2). Therefore predation by
gulls caused the disappearance of chicks.

5. Younger chicks were robbed preferably, more than expected, according
to age distribution (Fig. 9).

6. Hatching-, breeding- and fledging success (Fig. 8) increased with nest
density as the percentage of disappeared chicks decreased (Fig. 6, 7).

7. Breeding success is very low (Table 3: 0.2-0.4 chicks/nest).

Table 3. Nest, egg and chick numbers, chick fate and breeding success from 1979 to 1981

| | | 1979 | | 1980 | | 1981 | |
|---|---|---|---|---|---|---|---|
| | | Nests | Late nest | Nests | Late nests | Nests | Late nests |
| Egg loss | Nests | 81 | 40 | 126 | 47 | 164 | 55 |
| | Eggs | 219 | 86 | 344 | 87 | 432 | 88 |
| | Egg loss | 62 | 64 | 90 | 82 | 105 | 84 |
| | %Eggs | 28.3 | 74.4 | 26.2 | 94.3 | 24.3 | 95.5 |
| Hatching success | Chicks hatched | 156 | 22 | 254/243* | 5 | 327 | 4 |
| | %Eggs | 71.7 | 25.6 | 73.8 | 5.7 | 75.7 | 4.5 |
| Chick loss | Chicks disappeared | 107 | 16 | 106 | 2 | 207 | 4 |
| | %Chicks | 68.6 | 72.7 | 43.6 | 40.0 | 63.3 | 100.0 |
| | Chicks dead | 22 | 5 | 87 | 3 | 93 | - |
| | %Chicks | 14.1 | 22.7 | 35.8 | 60.0 | 28.4 | - |
| Fledging success | Chicks fledged ( 18T) | 27 | 1 | 50 | - | 27 | - |
| | %Chicks | 17.8 | 4.6 | 19.7 | - | 8.3 | - |
| Breeding success | %Eggs | 12.8 | 1.2 | 14.5 | - | 6.3 | - |
| | Per nest | 0.34 | 0.03 | 0.40 | - | 0.16 | - |
| Nest success | %Nests with 1 fle. | | | | | | |
| | Chick % nests | 28.4 | 2.5 | 31.7 | - | 15.9 | - |
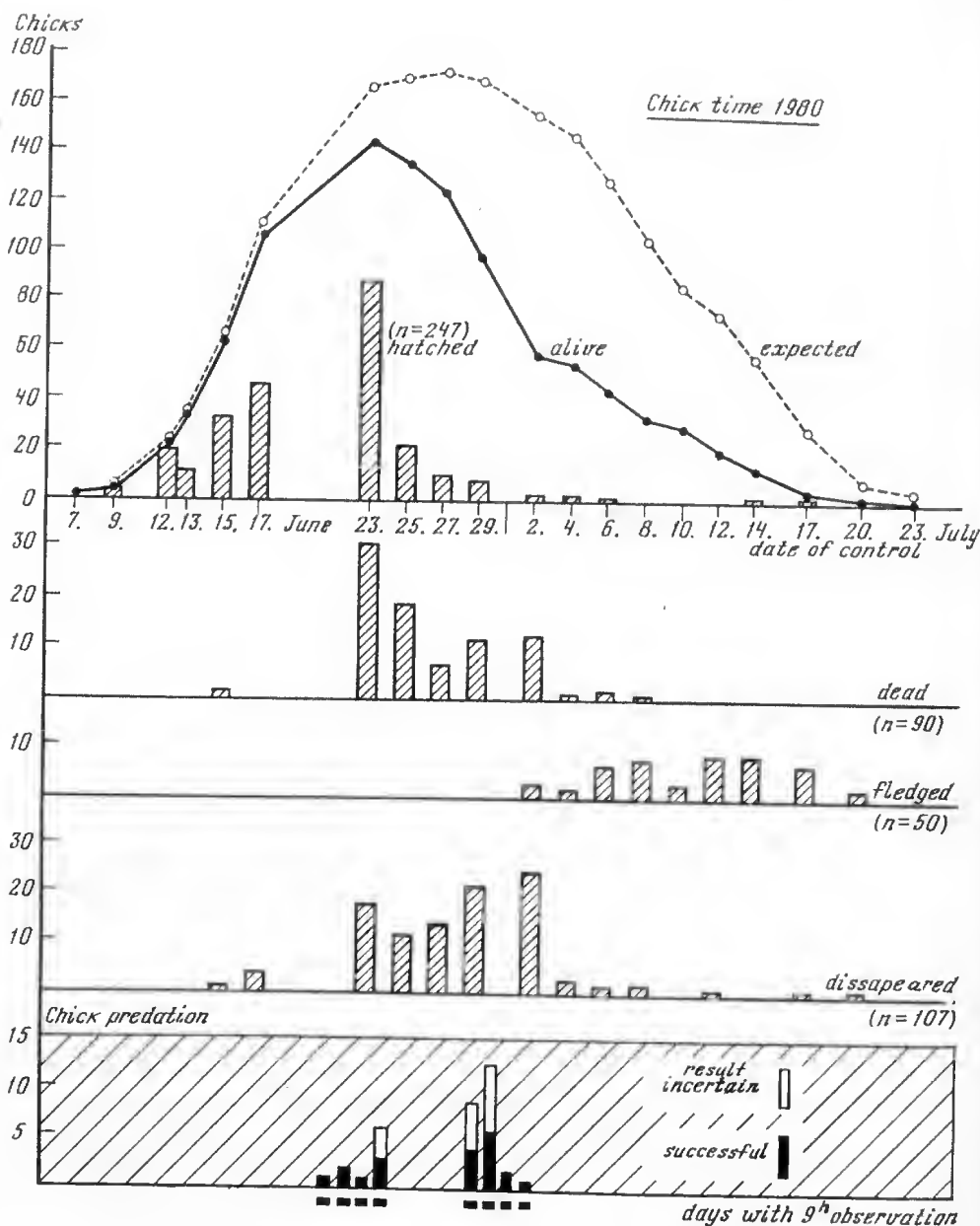
F i g. 4. Number and fate of chicks in 1980. Expected-hatched − (dead + fledged). Below: observations of chick predation by gulls

## DISCUSSION

Herring Gulls were the main factor for chick mortality. Although there was some compensation between mortality by other causes and by gulls (Fig.6, 7). the latter oppressed breeding success with 0.2-0.4 chicks/pair below the value necessary for maintaining colony size (after literature c. 1 chick/pair and year). Presumably the increasing number of breeding pairs is recruited by terns from other colonies.
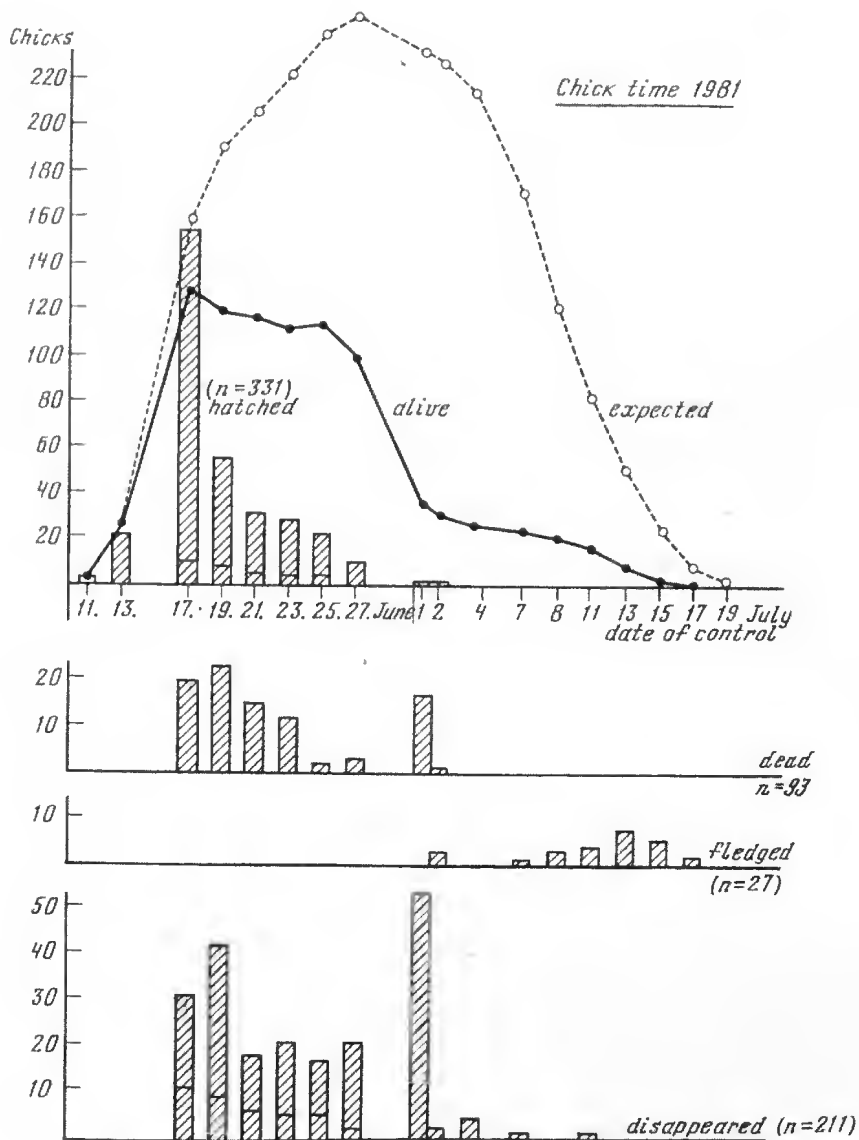
F i g. 5. As Fig. 4 for 1981

Decreasing breeding success with breeding time may be attributed to age and experience of the breeding birds. Early breeders select more favourable nest sites in areas with greater nest density, where defensive behaviour is more effective (Fig. 6, 7).

The course of chick predation shows that Herring Gulls were attentive to tern chicks not before hatching of a greater number Fig. 4). At about the same chick number predation fell down again (Fig. 4, 5); presumably predation on chicks wasn't effective any longer (small number, older chicks). This suggests that predatory gulls were not specialized in feeding on tern chicks.

F i g. 6. Chick fate in relation to nest density in 1980 (success: 11 days)

F i g. 7. As Fig. 6 for 1981
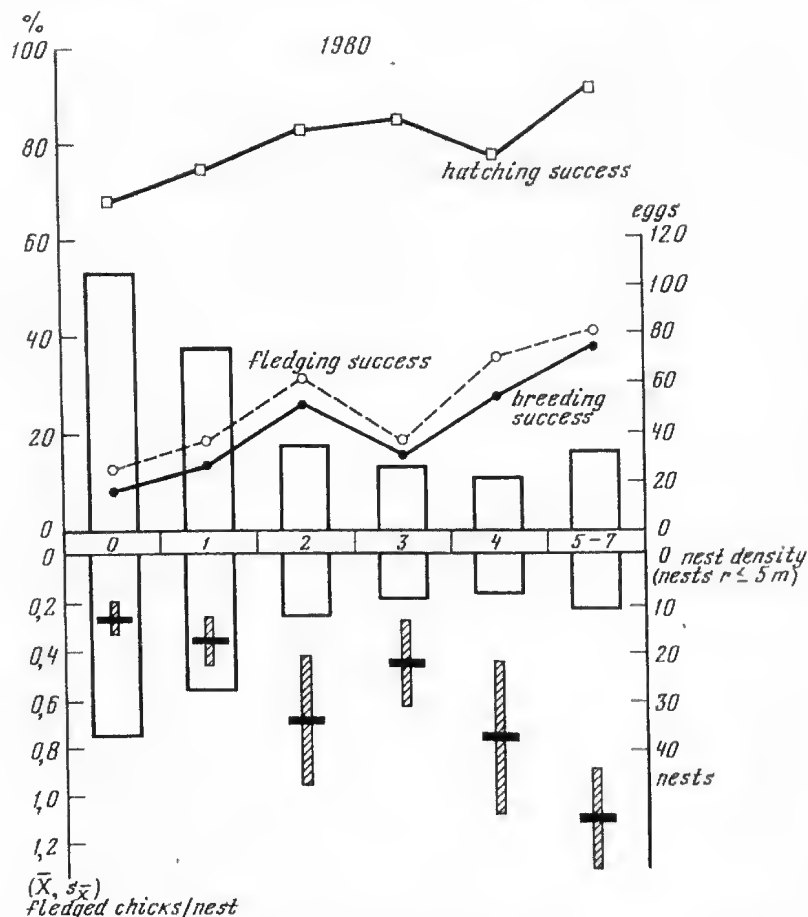


F i g. 8. Breeding success in relation to nest density (columns: eggs resp. nests)
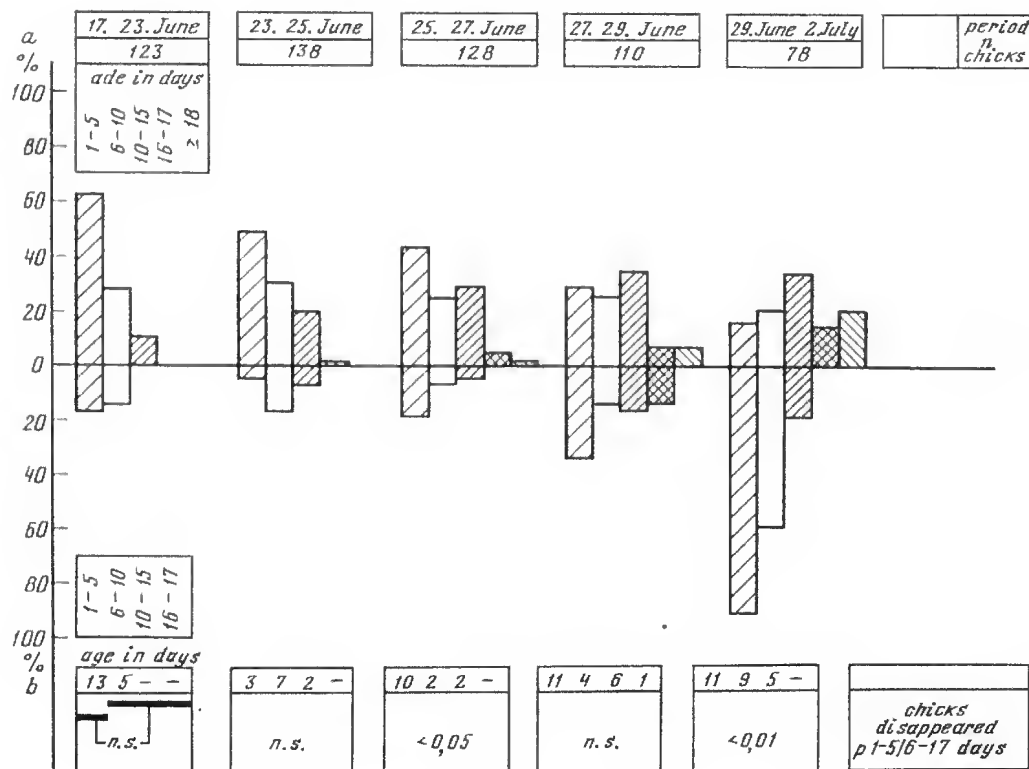
F i g. 9. Age distribution of a) chicks alive and b) chicks disappe-
ared during the breeding period in 1980. p – values: chicks disappe-
ared compared with the expected number according to a) $x^2$ test

SUMMARY

This study, started in 1979, is dealing with the breeding biology of a
little Common Tern colony (Sterna hirundo, 80-160 pairs), adjacent to a Her-
ring Gull (Larus argentatus) colony of about 10,500 pairs, on the Wadden Sea
island Mellum, FRG.        The results are based on records of marked
nests, eggs and chicks and on observations from a hide.

Egg loss by gulls occured rarely. But predation on chicks by Herring
Gulls was the main cause of the chick mortality increasing with advancing
breeding period. More than 40% of the chicks were robbed, mainly the younger
ones. The changes in frequency of chick predation during breeding time sug-
gest that the predatory gulls were not specialized in feeding on tern chicks.

The greater the nest density of terns the lower was the probability of
chick loss by gulls. Breeding success is negatively correlated with advanc-
ing time of egg laying and with nest spacing.

Due to predation by gulls the breeding success of Common Terns is low
(1979/1980/1981: 0.3/0.4/0.2 chicks/nest) and seems not to be sufficient to
maintain the size of the breeding colony.

DISTRIBUTION OF HERRING GULL EGG SIZE AND NEST DENSITY
IN THE MELLUM-COLONY IN RELATION TO VEGETATION HEIGHT

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STUDY AREA, AND METHODS

In 1979/1980 data were collected at the end of egg-laying-period of Her-
ring Gulls on 0,25 ha sample areas along a line transect through the breeding
colony Mellum, FRG (Fig. 1; in 1979: eastern areas, in 1980: western areas).
For measurements see Table 1. Breeding habitats are shown in Table 2.
For comparison of nest numbers per sample area between 1979 and 1981, study
plots at the eastern transect side were sampled again in 1981.

T a b l e  1. Measurements of nest vegetation and eggs

Nest measurements:

| | | |
|---|---|---|
| nest vegetation: | height | (cm) |
| | density | (% cover of the nestplace) |
| | surrounding | vegetation (degrees) |
| | index | (/height/max height + density/ max density + vegetation stand/ max vegetation stand/ : 3) |
| egg: | length | (mm) |
| | breadth | (mm) |
| | volume index | ($mm^3$; $breath^2$ x length) |
| | shape index | (breadth x 100/length) |

a) $\bar{x}$ nest
b) longest egg/nest
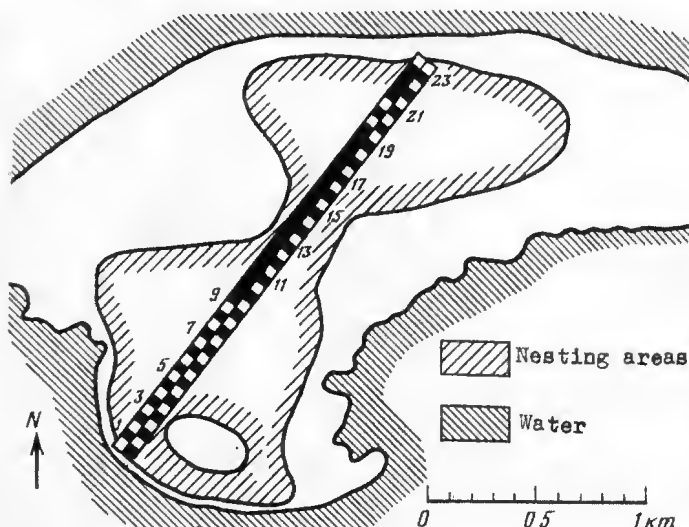


F i g. 1. The studied bre-
eding colony of Herring
Gulls on the Wadden Sea
island Mellum with line
transect and sample areas
(black, 0.25 ha)

Nesting areas
Water

RESULTS

1. Most Herring Gulls selected nest places with vegetation of 20-60 cm height, not covered by plants (only 0-10%) and with 40-90% of the nest circumference surrounded by vegetation (Fig.4).

2. Nest number per study plot was positively correlated with the vegetation measurements (Fig. 5 ).    With greater height of nest vegetation the number of breeding pairs decreased.

3. The distribution of mean values of nest vegetation and eggs is shown in table 2. In "Zwischensand", which is occasionally flooded, and the northern part of the "North dune", we found nests in sparse vegetation, greater egg dimensions and lower breeding pair density.

4. Egg length and volume decreased with vegetation height and index, egg length also with surrounding vegetation (Table 3). The shape-index was positively correlated with surrounding vegetation and index.

5. Looking at the means of sample areas (Table 4), egg length, breadth and volume were negatively correlated with nest vegetation measurements (except $\bar{x}$ egg breadth/density and surrounding vegetation). Two of these relations are plotted in Fig. 2-3.  .

6. In sample areas 3-9, the former colony center,and area 16, descreases in breeding pair numbers occurred from 1979-1981 ($\bar{x}$/year about - 16%). In areas 1, 22-23, however, where new breeding places originate from formation of dunes,we found increasing pair density ($\bar{x}$/year about +29%).
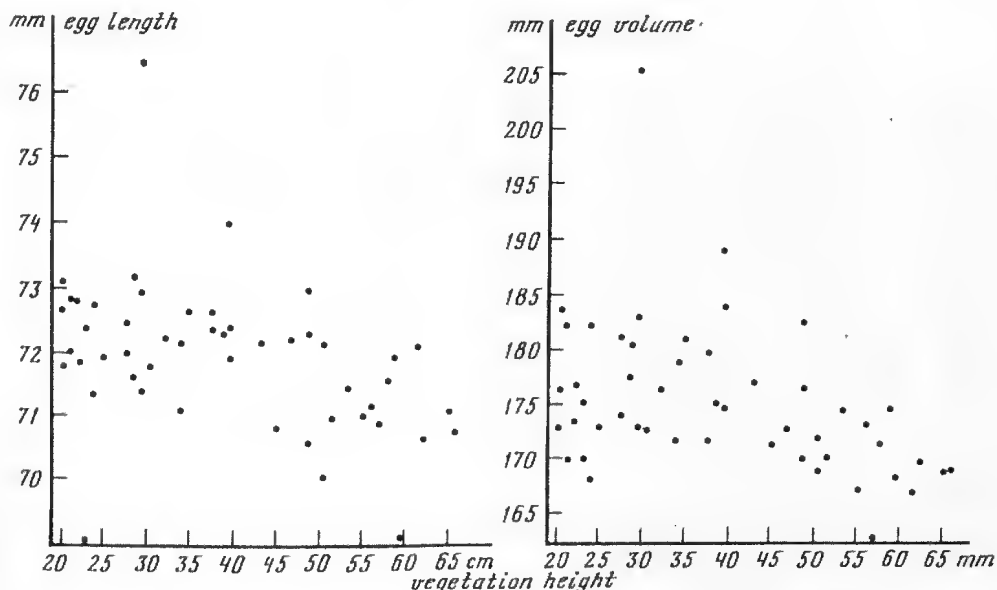


F i g s. 2, 3. Mean egg length and volume in relation to vegetation height at the nest (n = 50 areas)

T a b l e  2. Mean values of nest measurements per ha (2-3 sample areas) and greater than the median are underlined

| sample area | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
|---|---|---|---|---|---|---|---|---|---|---|
| nest number  per ha | 58 | 80 | 96 | 66 | 108 | 128 | 98 | 68 | 104 | 84 |
| nest number  change,% (79-81) | +80 | | -60 | -41 | -33 | -27 | -24 | +16 | -36 | |
| nest vegetation  height(cm) | 54 | 52 | 61 | 59 | 56 | 54 | 51 | 51 | 45 | 39 |
| nest vegetation  density(%) | 15 | 12 | 30 | 29 | 12 | 12 | 12 | 10 | 9 | 12 |
| nest vegetation  surrounding vegetation(°) | 204 | 219 | 265 | 273 | 262 | 236 | 235 | 249 | 221 | 241 |
| egg  length | 71.9 | 71,8 | 71,1 | 71,6 | 71,1 | 71,3 | 71,2 | 71,6 | 71,2 | 72,2 |
| egg  breadth | 49,2 | 48,9 | 49,1 | 48,3 | 48,9 | 49,1 | 49,0 | 48,8 | 49,1 | 49,3 |
| egg  volume | 178 | 172 | 171 | 167 | 171 | 172 | 171 | 171 | 172 | 177 |
| egg  shape index | 69,3 | 68,2 | 69,1 | 67,5 | 68,9 | 68,9 | 68,9 | 68,3 | 69,1 | 68,4 |
| n  nests measured | 29 | 40 | 48 | 33 | 54 | 64 | 49 | 34 | 52 | 63 |

T a b l e  3. Spearman correlation coefficients of egg and nest vegetation maeasurements (n = 790) p-values $^* \le$ 0.05, $^{**} \le$ 0.01, $^{***} \le$ 0.001. First value: $\bar{x}$ of eggs, nest, second value: longest egg/nest

| egg \ vegetation | height | density | surrounding vegetation | index |
|---|---|---|---|---|
| length | -0.11 [**]  -0.10 [**] | -0.07  -0.05 | -0.10 [**]  -0.10 [**] | -0.12 [***]  -0.11 [**] |
| breadth | -0.05  -0.03 | -0.03  -0.01 | -0.14  -0.03 | -0.03  -0.01 |
| volume | -0.09 [*]  -0.08 [*] | -0.05  -0.03 | -0.03  -0.02 | -0.07 [*]  -0.06 |
| shape index | 0.06  0.07 | 0.04  0.04 | 0.09 [**]  0.10 [**] | 0.08  0.08 [*] |

changes in breeding pair numbers from 1979 to 1981. Values

| 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 59 | 44 | 19 | 6 | 14 | 25 | 16 | 14 | 39 | 96 | 122 | 49 | 20 |
| | | | | | -43 | | | | | | +48 | +113 |
| 34 | 22 | 24 | 23 | 29 | 23 | 21 | 24 | 31 | 33 | 36 | 34 | 31 |
| 9 | 1 | 3 | 0 | 0 | 1 | 0 | 4 | 3 | 5 | 8 | 6 | 1 |
| 187 | 143 | 153 | 197 | 167 | 159 | 132 | 154 | 195 | 191 | 188 | 135 | 168 |
| 72,0 | 72,1 | 72,2 | 69,1 | 73,2 | 72,8 | 72,4 | 72,7 | 72,7 | 72,0 | 71,9 | 71,7 | 72,1 |
| 49,6 | 49,3 | 49,4 | 49,5 | 49,7 | 49,1 | 49,7 | 50,1 | 49,7 | 49,3 | 49,2 | 48,8 | 49,9 |
| 177 | 175 | 177 | 170 | 181 | 176 | 179 | 183 | 180 | 175 | 174 | 171 | 180 |
| 68,9 | 68,4 | 68,6 | 71,7 | 67,9 | 67,4 | 68,7 | 69,1 | 68,4 | 68,6 | 68,5 | 68,1 | 69,3 |
| 44 | 33 | 14 | 3 | 7 | 19 | 12 | 7 | 29 | 48 | 61 | 37 | 10 |

T a b l e  4. Spearman correlation coefficients of egg and nest vegetation means per sample area (n = 50; p-values, first and second value as in Table 3). See also Fig. 2, 3

| egg \ vegetation | height | density | surrounding vegetation | index |
|---|---|---|---|---|
| length | -0.47*** | -0.34* | -0.34* | -0.44** |
| | -0.46*** | -032* | -0.34* | -0.43** |
| breadth | -0.34* | -0.23 | -0.20 | -0.28* |
| | -0.35* | -0.31* | -0.27 | -0.31* |
| volume | -0.47*** | -0.33* | -0.35* | -0.43** |
| | -0.45** | -0.36* | -0.38** | -0.43** |
| shape index | 0.14 | 0.18 | 0.14 | 0.18 |
| | 0.12 | 0.02 | 0.06 | 0.11 |
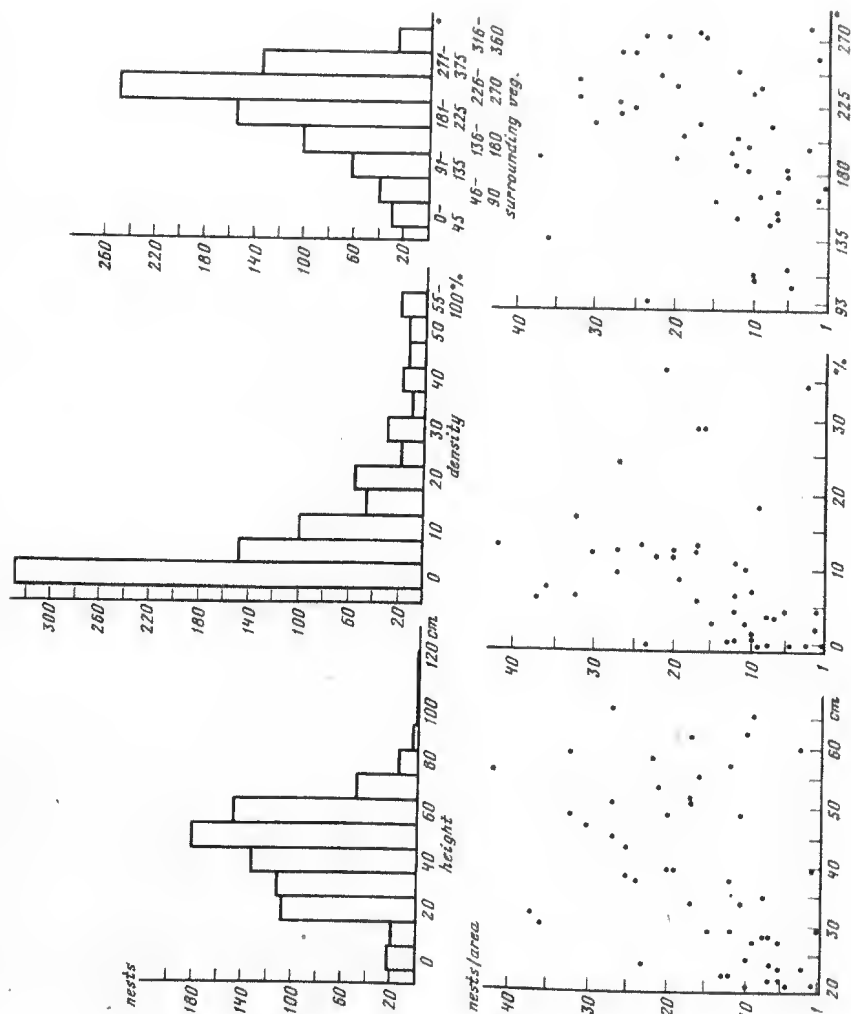
F i g. 4. Frequency of nests over height (a), density (b), surrounding stand of vegetation (c) at the nest

F i g. 5. Number of nests/sample area (a), (n = 50) in relation to mean values of nest-vegetation height (p < 0.001) (b), surrounding vegetation (p < 0.01) (c). Spearman correlation coefficients

## DISCUSSION

We can explain these results by age related differences in egg size. In larids first breeders have smaller eggs; the size of old females' eggs of many bird species becomes smaller again. Unfortunately, we have only some suggestions for this in larids.

Herring Gulls show fidelity to their nest site, which is characterized by growing vegetation over years on Wadden Sea islands. Therefore older pairs with smaller eggs may breed in nesting areas with higher and denser plant cover (area 3-9, the former colony center). The earliest time "Zwischensand" could be colonized by presumably younger birds was about 10 years ago. Now these birds being mature occupy the small number of possible nest places. This is why we find on an average bigger eggs in these areas.

Birds breeding for the first time, but also resettling birds, will prefer optimal breeding areas, great nesting density and the edge of the colony for breeding (areas 1, 2, 21-23). Therefore we found reduced means of egg size in such regions.

## SUMMARY

About 10,500 Herring Gulls pairs (_Larus argentatus_) are breeding on the Wadden Sea Island Mellum,    FRG        Due to formation of dunes and changes in vegetation the population is expanding and increasing during the last years.

Data from Herring Gull nests were collected in 1979/80 on 50x50 m sample areas placed along a line transect, running through the typical zones of nest density and vegetation.

Nest sites in high or low vegetation are avoided by the Herring Gulls. There is a decrease in nest numbers in areas with high vegetation within a period of two years.

Egg size (length, breadth, volume) is negatively correlated with vegetation-height and -density at the nest. We explain this by the age of breeding females, nest site tenacity and nest site choice.

CHARACTERISTICS OF SOME BIRD SPECIES MIGRATIONS
ACCORDING TO THE RINGING DATA

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The great part of peculiarities of the seasonal distribution, ways of
migration and wintering places of the birds from different populations be-
comes clear due to the investigation of the repeated recoveries of the ringed
birds as a result of ringing and marking of birds. In this paper  some pecu-
liarities of migration of 5 bird species of different orders and type of mig-
rations are examined: Goldeneye (Bucephala clangula), Lapwing (Vanellus vanel-
lus), Robin (Erithacus rubecula), Great Tit (Parus major), Brambling (Frin-
gilla montifringilla).

MATERIAL AND METHODS

The repeated recoveries of the ringed birds of both sexes and different
age have laid down the foundations for the present work. 175 recoveries of
Bucephala clangula, 256 of Vanellus vanellus, 105 of Erithacus rubecula, 236
Parus major and 313 of Fringilla montifringilla were used for the work. The
recoveries of birds ringed in the USSR and found both on the territory of the
USSR and abroad as well as the recoveries of birds ringed overseas and found
in the USSR were used for the work.

RESULTS

Bucephala clangula. The goldeneye ringed in the Murmansk region (mainly
in the Lapland and in the Kandalaksha Reserves) have two migratory routes
(Fig. 1). In autumn some of the birds fly along the western seashore of the
Baltic Sea and spend winter mainly in Denmark, others fly along the eastern
shore of the Baltic Sea and winter either in south-western or western Europe,
or in southern and south-western regions of the USSR European part.

The ringing of the goldeneye in the Arhangelskaya, Kalininskaya, Vologod-
skaya and Leningradskaya regions of the USSR has indicated that birds from
these regions winter mainly in central and southern Europe and in the south-
western districts of the USSR. More northern populations of birds winter more
northwards than the southern ones.

The ringing of the goldeneye in more eastern districts of the USSR (Komi
ASSR, the Chelyabinskaya region) has shown more eastern areas of their wint-
ering sites: in south-western and southern districts of the USSR.

The chief directions of the goldeneye's migration is south-west and south-
wards. Speed of their autumn flight is up to 80 km per day.

Vanellus vanellus (Fig. 2). The lapwing banded in the Leningradskaya regi-
on, in Estonian, Latvian and Lithuanian SSR and in the Okski Reserve in the
Ryazanskaya region spend winter in Holland, Belgium, northern parts of Italy,
in Spain and in the North of Africa (in Algiers, Morroco), though most of
them winter in the western parts of France.
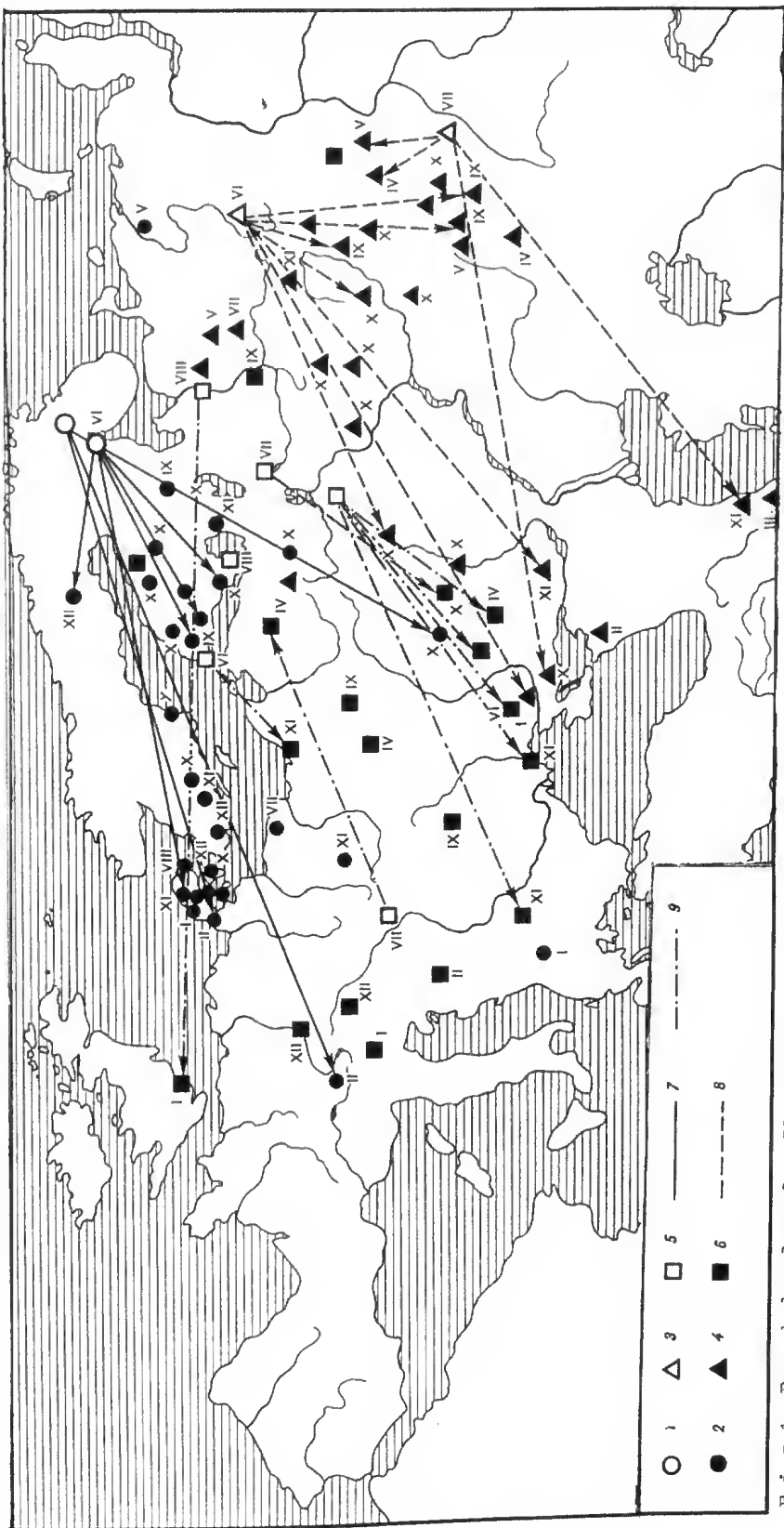
F i g. 1. Bucephala clangula. Places of ringing birds and meeting places of banded birds
1 - Places of ringing birds in Murmanskaya region. 2 - Places where birds mashed in the Murmanskaya region
meet. 3 - Places of ringing birds in Komi ASSR and the Chelyabinskaya region. 4 - Meeting places of birds
marhed in Komi ASSR and the Chelyabinskaya region. 5 - Places for ringing the goldeneye in the rest of USSR
European part. 6 - Meeting places of birds banded over the rest of the USSR European part. 7-9 - Direct recoveries.
The arrow indicates direct recoveries. The Roman members indicate the months of ringing and recoveries - repeated
finds of banded birds

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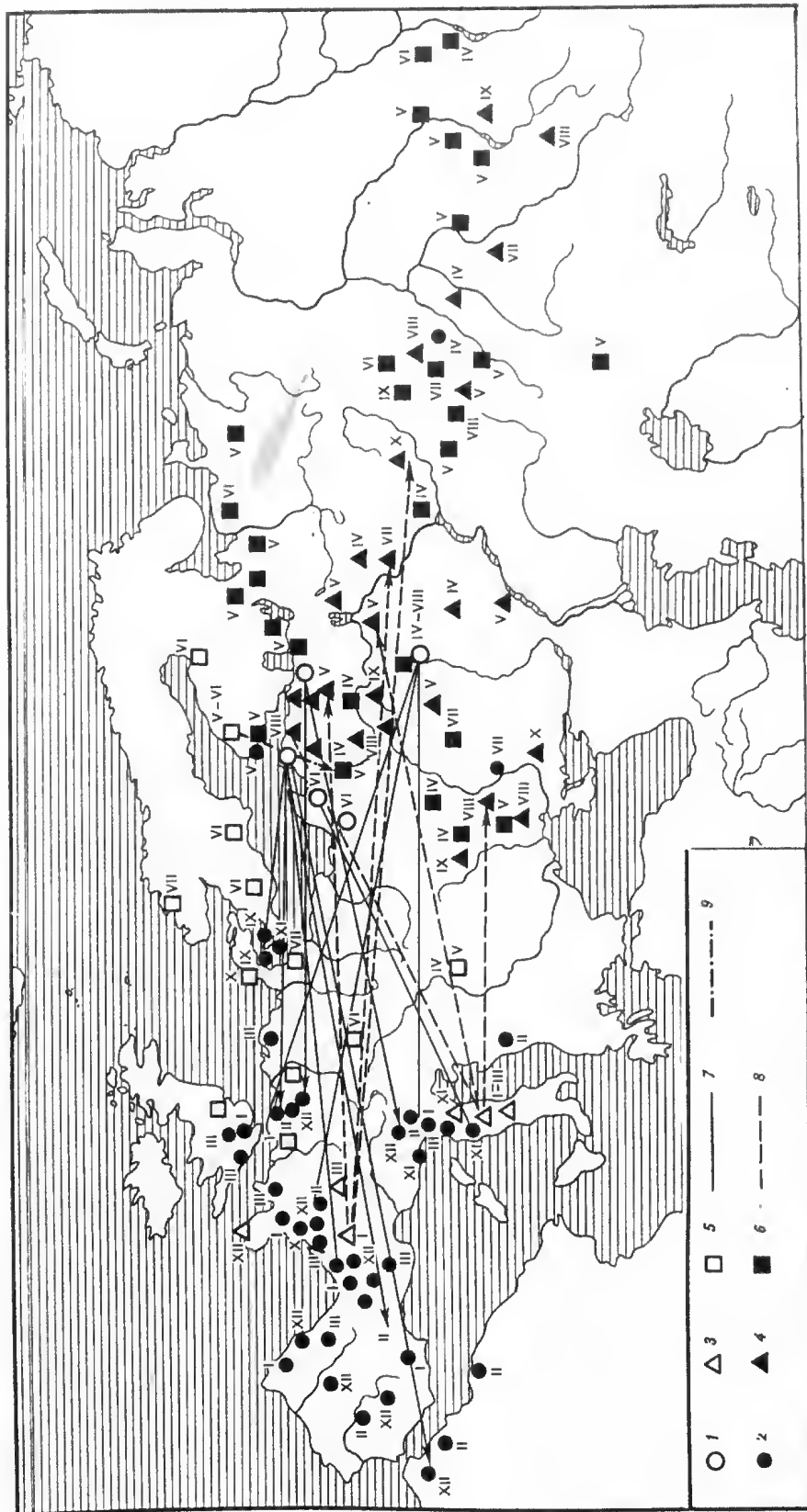
F i g. 2. Vanellus vanellus. Places of ringing and meeting places of marked birds
1- Places of ringing birds in the USSR. 2- Meeting places of birds ringed in the USSR. 3 - Places of ringing
birds in France and Italy. 4 - Meeting places of birds banded in France and Italy. 5 - Places of ringing the
lapwing in Scandinavia, England, Belgium, Holland, FRG, GDR and Hungary. 6 - Meeting places of birds ringed in
Scandinavia, England, Belgium, Holland, FRG, GDR and Hungary. 7-9 - Direct recoveries

The lapwings marked in England whan on route in autumn and spring wers later seen in western and central regions of the USSR European part and even in the Tyumen region. Birds marked in the Scandinavian countries are mostly observed in north-western districts of the USSR European part; some - in the central districts of the USSR European part, part of them in the central districts of the USSR European part and even in the Novosibirsk region.

The lapwings banded on their wintering sites in Holland, Belgium, France and Italy and while en route in spring and autumn over GDR, FRG, Hungary were then obgerved mostly in western, northern and central districts of the USSR European part as well as in the Kazahskay SSR and Siberia including ths Tymenskaya, Tomskaya regions and the Krasnoyarsky district. The farthsst recoveries are from Holland and Belgium and less distant recoveries are from France and Italy.

In spring the lapwings coming back to their nesting sites might take different routes, their finding themselves either in Scandinavian countries or in south-western districts of the USSR.

Erithacus rubecula (Fig. 3). Ths robins banded in the north-western districts of the USSR European part are seen on the territory of Poland, GDR, FRG, Holland, Belgium, but most of the recoveries of wintering banded birds are from southern France, central Italy, Corsica, Sardinia and Spain. In reality there are no differences in the territorial distribution of recoveries from various areas though there was observed a tendency for the robins marked in Latvia and the Kaliningradskaya region to winter somewhat more southwards as compared to birds banded in other localities. Part of the robins winter in northern Africa (Morocco, Algiers, Tunis) and Turkey. The wintering sites of adult birds as a rule are situated in more northsrn districts than those of the young birds. There is evidence to the fact that robins in different years in autumn might fly along different sides of the Baltic Sea (either through the USSR or through Sweden),they might radically change the routes and wintering sites.

Parus major (Fig. 4). Wide ringing of the Great Tit in the USSR shows that these birds are not only resident or travelling short distances but that they fly considerable distances espectally when they are young.

The great tits marked in the Karelian ASSR, Leningradskaya, Pskovskaya regions and in the Estonian SSR were seen en route and in winter in Finland, Poland, GDR, Holland, Belgium and in the north of France.

The birds banded in the Lithuanian and Beylorussian SSR reach central and southern districts of France and Portugal which means that the more northern populations of the great tit winter more northwards than the southern ones.

Mean speed of the great tit is about 20 km per day.

Fringilla montifringilla (Fig. 5). Bramblings ringed in the Murmanskaya region (the Lapland and Kandalaksha Reservss), the Leningradskaya, Pskovskaya regions, the Latvian and Lithuanian SSR in most cases take the Italo-Spanish migratory route south-south-westwards to northern Italy, southern France and Spain.

The bramblings marksd in the Kaliningradksaya region have two migratory routes. Some, mostly adult birds, take the so-called seashore route, west-
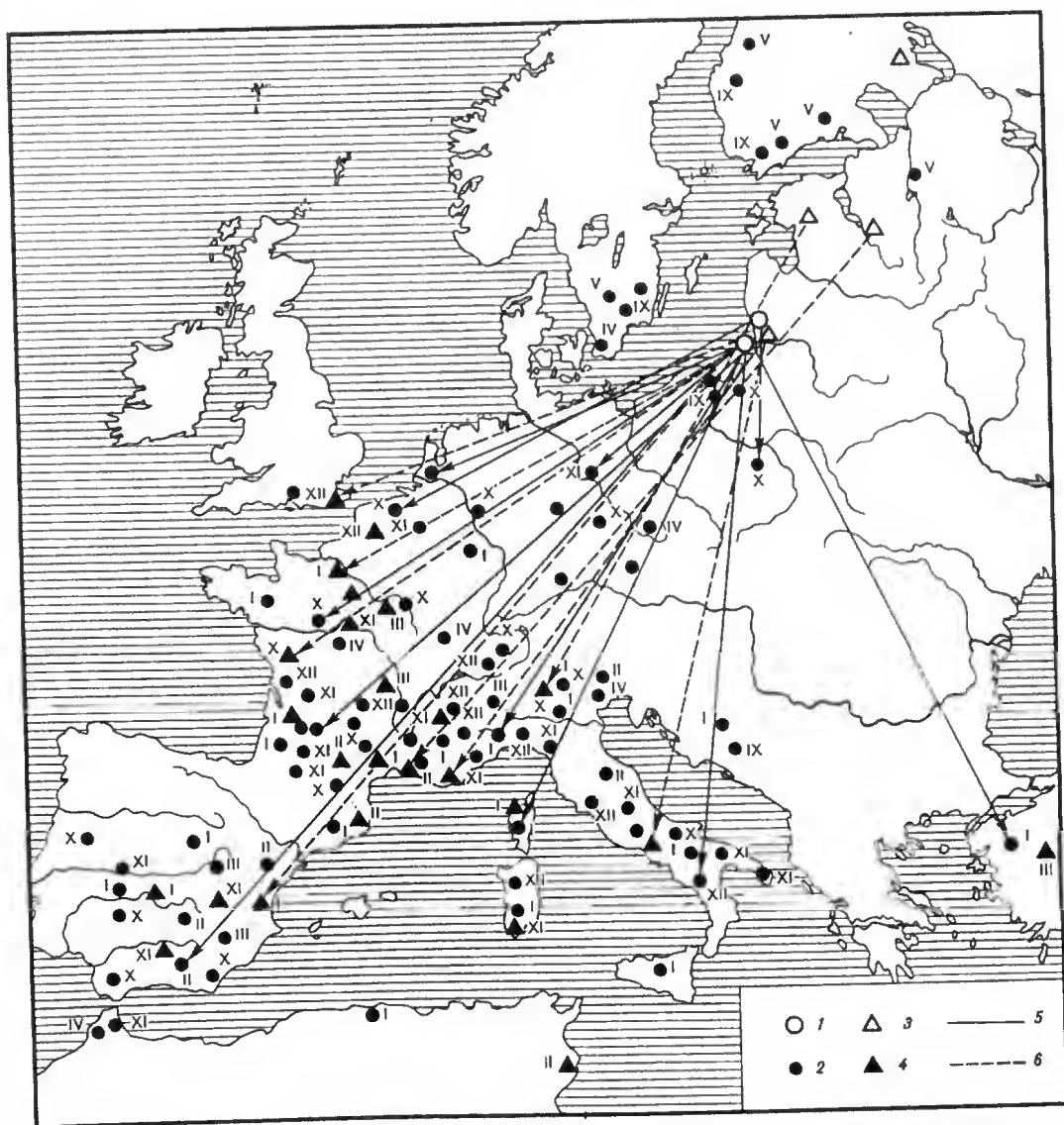
F i g. 3. Erithacus rubecula. Places of ringing birds and meeting places of banded birds

1 – Places of ringing the robin in the Latvian SSR and the Kaliningradskaya region. 2 – Meeting places of birds ringed in Latvia and the Kaliningradksaya region. 3 – Places of ringing birds in the other districts of the north-western area of the USSR European part. 4 – Meeting places of birds ringed in north-western districts of the USSR European part, except Latvia and the Kaliningradskay region. 5,6 – Direct recoveries

south-westwards across the northern and central parts of the GDR, FRG, Holland and Belgium. Others, mostly young birds, fly the Italian-Spanish route. Later on these birds might spread into the central and southern France. Then, closer to spring time they more over to Switzerland, FRG, Czechoslovakia and
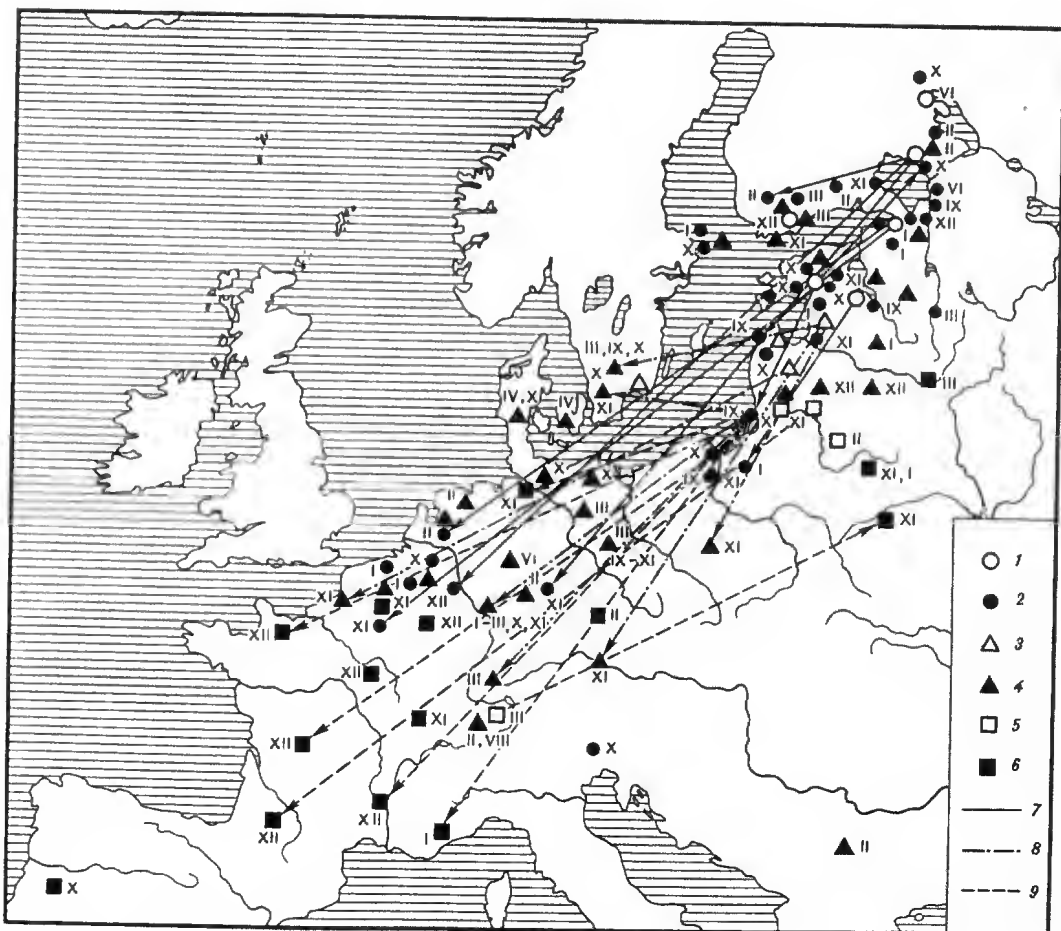
F i g. 4.

Parus major. Places of ringing birds and meeting places of ringed birds

1 - Places of ringing the great tit in Karelian SSR, the Lenin-
    gradskaya, Pskovskaya regions and in the Estonian SSR.

2 - Meeting places of birds ringed in Karelia, the Leningradskaya
    and Pskovskaya regions and in Estonia.

3 - Places of ringing birds in the Latvian SSR and the Kalinin-
    gradskaya region.

4 - Meeting places of birds ringed in Latvia and Kaliningradskaya
    region.

5 - Places of ringing birds in the Lithuanian and Beylorussian
    SSR.

6 - Meeting places of birds ringed in the Lithuanian and Beylo-
    russian SSR.

7-9 - Direct recoveries
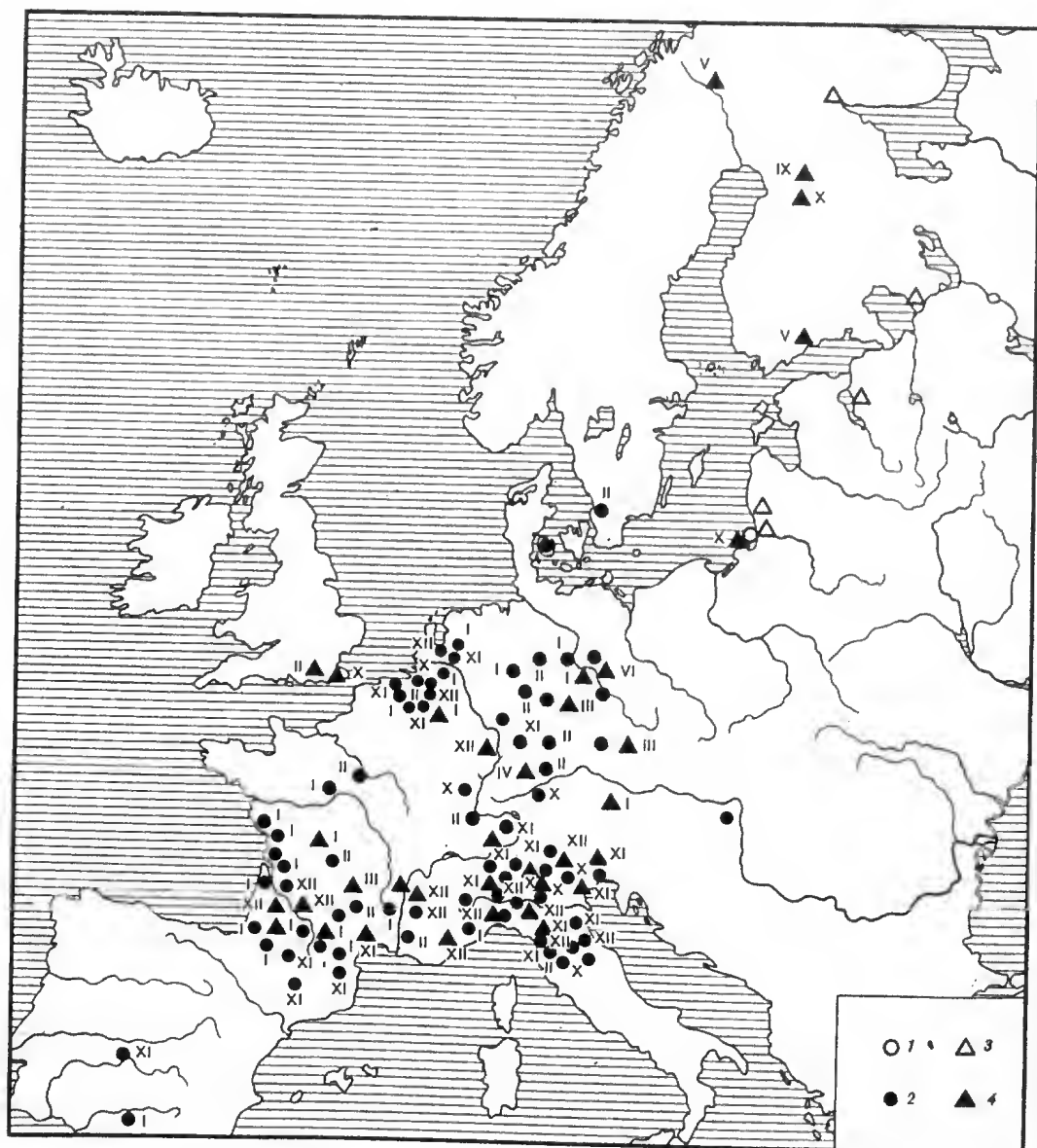
F i g. 5.
<u>Fringilla montifringilla</u>. Places of ringing the brambling and
meeting places of banded birds
1 – Place of ringing the brambling in the Kaliningradskaya
    region (Rybachii).
2 – Meeting places of birds ringed in Rybachii.
3 – Places of ringing the brambling in the other districts of
    north-western USSR European part.
4 – Meeting places of birds ringed in the other districts of
    north-western USSR European part

Poland. Bramblings which spend winter in the western Europe might change their routes and wintering sites in various years.

Mean speed of bramblings' autumn migration is 45-50 km per day.

SUMMARY

The paper deals with the results of recoveries received by the Center of Ringing of Birds. The species were those ringed on a mass scale; they were: Bucephala clangula (Anseriformes), Vanellus vanellus (Charadriiformes); Erithacus ribecula, Parus major, Fringilla montifringilla (Passeriformes).

All the examined species marked in the north-west regions of the USSR European region winter in central and south-west countries of Western Europe, some of them - as far as Spain (the lapwing, the robin, the brambling), Portugal and countries of Northern Africa (the lapwing, the robin).

Birds which are marked in more eastern regions of the USSR winter mainly in south-western and southern parts of the USSR European part.

Birds marked in more southern areas, spend winter more southwards than those marked in more northern districts.

In all species individuals of both sexes migrate simultaneously and winter in the same localities.

In all species we observed young birds winter more southwards than adult ones.

All bird species which have fixed migratory routes, wintering and nesting sites might change them depending on age, weather conditions and other reasons. Different populations of birds might have the same or different migratory routes, wintering and nesting areas. For instance, the goldeneye of the Murmansk region (USSR) in winter flies along either the western or the eastern shore of the Baltic Sea. The lapwings might fly back to their nesting sites by different routes coming either to the Scandinavian countries or to the north-western districts of the USSR. Robins might also fly along different sides of the Baltic Sea, changing their flying routes and wintering sites. Bramblings from more southern areas of the north-west district of the USSR (the Kaliningrad district) have two migratory routes. Some of them, mostly adult birds, take the seashore migratory route west-south-west bound. Year in, year out bramblings wintering in western Europe might also change routes and wintering sites.

ENERGY OF EXISTENCE AT 0° AND 30° AND BASAL METABOLISM
OF INSECTIVOROUS AND GRANIVOROUS <u>PASSERIFORMES</u>: THEIR
SEASONAL CHANGE AND DEPENDENCE ON BODY MASS

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The present paper is concerned with energy requirements of <u>Passeriformes</u> consuming different kinds of food, i.e. granivorous and insectivorous. Analysis is performed of different parameters of their bioenergetics: energy of existence at different ambient temperatures and basal metabolism. Not only species differences are analyzed but also those between groups of species forming a particular size series. Analysis is aimed at revealing the relationship between metabolic rate and body mass described in a general form as a power function $M = am^b$ where M, metabolic rate index, m, body mass; a sets the elevation of regression line, and b, its slope. All the regression equations are calculated using the method of least squares.

MATERIAL AND METHOD

52 passerine species mostly captured at the Kurische Nehrung (the Baltic Sea) were used. All the birds were maintained in open-air cages from 1 to 4 weeks prior to the beginning of experiments, in which they were exposed to ambient temperatures and photoperiod characteristic of the given site. Tropical, subtropical and warm zone wintering birds (i.e. migrating to warm zones from October to May) were maintained at 12-22°C. In winter (from December to February) only non-moulting birds were used in experiments; in spring wild birds were measured in late April - early May, i.e. towards the end of or at the end of migration to the north. In summer measurements were made in late June - early July, i.e. between the termination of breeding and initiation of moult. Fringillidae and Proceidae were used in experiments during moult and breeding -free periods in summer and in winter.

Both winter and summer measurements were made only for part of the species under study.

Oxygen consumption was measured in fasting birds during the night. Large birds were made to fast beginning at noon; the smaller ones - 3-4 hours before dark. Each bird was put into a small cage and subsequently into an acryl plastic chamber in the dark. The chambers varied in size from 3 to 1 depending on the bird size. The air flow through the chamber was regulated, and, following stabilization of the temperature, switched to the recording instruments. Actual measurements of oxygen consumption were started 2-3 hours after dark and completed 1-2 hours before dawn. Each experiment lasted from 1 to 4 hours. The rate of basal metabolism was determined as a mean value obtainted for the zone of thermoneutrality (1 $cm^3 O_2$ = 20.1 J).

Energy of existence was measured at 3-6 different ambient temperatures, mostly from 0° to 30°, occasionally - up to -10° (in winter). Small birds were maintained in 40X30X25 cm cages, medium size birds - in 150X75X75 cm cages. A single experiment lasted 3-4 days and occasionally daily experiments were performed (if during that time the weight of the experimental birds did not change). The birds were weighed early in the morning

(before dawn), at the beginning and at the end of measurements. If body
weight changes were insignificant, corrections were made, using the calorific
equivalent of body weight change 25.122 kJ/g (Dolnik, Gavrilov, 1971). If
body weight changes were considerable, these data were neglected. The insec-
tivorous birds were fed with boiled homogenized hen eggs, which were thinly
sliced (25.75 kJ/g of dry mass) and flour worms; granivorous birds were given
various seeds, mostly of cultivated plants.

RESULTS AND DISCUSSION

Basal metabolism was measured in relation to oxygen consumption rate after
a brief period of fasting. Food assimilation did not take place, and the ma-
jor source of energy was fat oxidation. This is indicated by the low respi-
ration coefficient. The understanding of how basal metabolism is changed in
birds consuming different kinds of food is the groundwork on which are
based energy requirements for all other types of activity, normal existence
including.

Our measurements of the level of basal metabolism in all the 52 passerine
species under study separately for two seasons (winter and summer) are pre-
sented in Tables 1,2,Fig1. In species,for which data are available both for
winter and summer, basal metabolism is largely higher in winter than in sum-
mer. This is mostly characteristic of granivorous birds. An increase in basal
metabolism in winter is one of the major adaptations to climate seasonality
(Gavrilov, 1979, 1980a,b, 1982). These adaptations are naturally more pro-
nounced in northern birds, which invariably include more granivorous species.
The scanty data on respiration coefficient available indicate that it is
practically similar within a single season in all the species under study.
In winter it is somewhat lower than in summer. This is indicative of a great-
er proportion of fats utilized at that period.

The energy of existence (EM) is the rate of metabolism at which energy is
utilized by cage birds retaining a constant body weight during a certain
period free of productive processes, e.g. moult, migration agitation, growth
or fat storage. Species, for which data are available for both winter and
summer seasons, display energy of existence which is higher both at 0° and
30°C in summer. This is explained by the fact that the total amount of met-
abolized food is larger under a longer summer photoperiod (Table 1, 2,Fig.1),
on the one hand, and as to the 30° value, it is accounted for by a decline
in heat conductivity of the integuments.

The energy of the same avian species at the same body temperature varies
with diet (species were tested which consume both animal and grain foods)
(Table 3). On grain diet food consumption increases both in summer and in
winter, the summer increase being greater compared with winter. This is ac-
counted for by the fact that utilization coefficient for different foods
varies seasonally. The birds under study normally turn to feeding on insects
in summer (except the nutcracker); hence, feeding on grain diet decreases
their coefficient of food utilization. Nevertheless, feeding on grain diet
provides more energy, and this additional energy must be dissipated.

The relationship between bioenergetic indices and body mass (Table 4,
Fig. 2) - data on Estrildinae are excluded from the equations - is indicat-

T a b l e  1. Summer measurements of bioenergetic parameters in passerine birds

| Species | Body mass, g | $EMR_{0°}$ | h | $EMR_{30°}$ | BMR |
|---|---|---|---|---|---|
| Phylloscopus sibilatrix | 7.6 | 57.8 | 1.14 | 23.5 | 15.1 |
| Estrilda troglodytes | 7.7 | 67.0 | 1.48 | 22.6 | 13.0 |
| Tiaris canora | 7.8 | 67.4 | 1.44 | 24.3 | 13.4 |
| Aegithalos caudatus | 8.8 | 62.0 | 1.22 | 25.4 | 17.2 |
| Troglodytes troglodytes | 9.0 | 62.4 | 1.18 | 26.8 | 18.4 |
| Uraeginthus bengalis | 9.2 | 66.0 | 1.35 | 26.8 | 13.4 |
| Parus ater | 9.7 | 65.3 | 1.23 | 28.4 | 20.5 |
| Phylloscopus trochilus | 9.8 | 68.2 | 1.59 | 20.5 | 18.0 |
| Lonchura striata | 10.3 | 71.6 | 1.37 | 30.5 | 17.2 |
| Sylvia curruca | 10.3 | 68.2 | 1.24 | 30.9 | 17.2 |
| Parus palustris | 11.1 | 67.8 | 1.17 | 32.7 | 19.0 |
| Acrocephalus schoenobenus | 11.5 | 72.8 | 1.34 | 32.7 | 18.8 |
| Spinus spinus | 12.0 | 68.7 | 1.10 | 35.8 | 25.1 |
| Serinus canaria | 12.8 | 70.6 | 1.34 | 30.5 | 18.0 |
| Acanthis flammea | 13.5 | 71.2 | 1.05 | 39.5 | 24.7 |
| Phoenicurus ochruros | 14.0 | 77.9 | 1.37 | 36.8 | 20.9 |
| Erithacus rubecula | 14.0 | 78.7 | 1.45 | 33.1 | 26.0 |
| Hippolais icterina | 14.1 | 80.4 | 1.45 | 36.8 | 21.8 |
| Motacilla flava | 15.4 | 81.6 | 1.38 | 40.2 | 22.2 |
| Saxicola rubetra | 15.7 | 82.9 | 1.39 | 41.1 | 20.9 |
| Anthus pratensis | 17.5 | 89.6 | 1.59 | 41.9 | 26.0 |
| Motacilla alba | 18.0 | 87.1 | 1.43 | 44.1 | 26.0 |
| Sylvia atricapilla | 20.0 | 97.1 | 1.75 | 44.8 | 33.0 |
| Sylvia nisoria | 20.6 | 101.3 | 1.81 | 46.9 | 33.1 |
| Carpodacus erythrinus | 21.0 | 110.5 | 1.75 | 58.2 | 31.8 |
| Passer d. bactrianus | 22.2 | 110.1 | 1.77 | 57.0 | 31.8 |
| Passer domesticus | 25.0 | 103.4 | 1.31 | 64.2 | 41.0 |
| Lanuis collurio | 25.3 | 101.3 | 1.39 | 59.5 | 33.1 |
| Chloris chloris | 26.5 | 108.0 | 1.37 | 66.9 | 41.0 |
| Emberiza hortulana | 26.5 | 114.7 | 1.74 | 62.6 | 36.0 |
| Emberiza citrinella | 27.1 | 112.6 | 1.73 | 60.7 | 37.7 |
| Loxia curvirostra | 44.7 | 135.6 | 1.39 | 93.8 | 51.9 |
| Oriolus oriolus | 65.1 | 169.1 | 2.22 | 102.6 | 56.1 |
| Turdus philomelos | 80.0 | 218.1 | 2.92 | 130.6 | 62.8 |
| Turdus merula | 83.0 | 193.9 | 1.93 | 135.8 | 80.4 |

T a b l e  2. Winter measurements of bioenergetic parameters in passerine birds

| Species | Body mass, g | $EMR_{\male}$ | h | $EMR_{3\male}$ | BMR |
|---|---|---|---|---|---|
| Aegithalos caudatus | 8.8 | 60.7 | 1.09 | 28.1 | 21.8 |
| Troglodytes troglodytes | 9.0 | 58.6 | 0.96 | 29.7 | 20.9 |
| Parus ater | 9.7 | 62.0 | 1.05 | 36.6 | 23.4 |
| Phylloscopus trochilus | 9.8 | 66.1 | 1.23 | 29.4 | 18.0 |
| Ficedula hypoleuca | 11.2 | 70.3 | 1.30 | 31.3 | 20.1 |
| Phoenicurus phoenicurus | 11.6 | 69.1 | 1.18 | 33.5 | 20.1 |
| Spinus spinus | 12.0 | 66.6 | 0.99 | 36.8 | 28.5 |
| Serinus canaria | 12.2 | 70.3 | 1.05 | 38.9 | 19.7 |
| Acanthis flammea | 13.5 | 67.4 | 1.00 | 37.3 | 29.3 |
| Erithacus rubecula | 14.0 | 76.2 | 1.34 | 36.0 | 24.3 |
| Acanthis cannabina | 14.5 | 79.5 | 1.34 | 39.4 | 29.3 |
| Carduelis carduelis | 15.9 | 78.7 | 1.18 | 43.2 | 30.1 |
| Motacilla alba | 18.0 | 82.1 | 1.36 | 41.4 | 24.3 |
| Emberiza schoeniclus | 18.2 | 87.1 | 1.39 | 45.3 | 26.0 |
| Luscinia svecica | 18.2 | 90.4 | 1.59 | 42.7 | 31.0 |
| Fringilla montifringilla | 21.0 | 94.6 | 1.37 | 53.5 | 33.1 |
| Carpodacus erythrinus | 21.0 | 98.4 | 1.60 | 50.3 | 31.0 |
| Sylvia borin | 22.0 | 95.9 | 1.45 | 52.3 | 36.0 |
| Passer d. bactrianus | 22.2 | 96.7 | 1.56 | 49.9 | 31.8 |
| Passer domesticus | 25.0 | 98.8 | 1.14 | 64.5 | 42.3 |
| Passer montanus | 22.5 | 97.1 | 1.56 | 50.3 | |
| Anthus campestris | 23.1 | 101.3 | 1.59 | 53.6 | |
| Anthus trivialis | 23.2 | 104.3 | 1.79 | 50.6 | 29.3 |
| Chloris chloris | 26.5 | 98.4 | 1.29 | 59.7 | 48.1 |
| Emberiza hortulana | 26.5 | 107.2 | 1.59 | 59.5 | 35.2 |
| Emberiza citrinella | 27.1 | 101.7 | 1.30 | 62.7 | 43.1 |
| Pyrrhula pyrrhula | 30.4 | 110.1 | 1.56 | 63.6 | 47.7 |
| Loxia curvirostra | 44.7 | 128.1 | 1.24 | 90.8 | 58.2 |
| Coccothraustes coccothraustes | 48.2 | 141.9 | 1.64 | 92.6 | 60.3 |
| Loxia pytiopsittacus | 53.4 | 138.2 | 1.16 | 103.4 | 69.1 |
| Turdus iliacus | 57.0 | 157.0 | 2.09 | 94.2 | 62.4 |
| Lanius excubitor | 71.3 | 177.1 | 2.27 | 108.9 | 70.3 |
| Sturnus vulgaris | 78.0 | 179.2 | 2.05 | 117.6 | 77.5 |
| Turdus philomelos | 80.0 | 187.2 | 2.55 | 110.5 | 65.3 |
| Turdus merula | 83.0 | 180.9 | 1.91 | 123.5 | 89.6 |
| Turdus viscivorus | 112.0 | 223.6 | 2.52 | 147.8 | 95.5 |
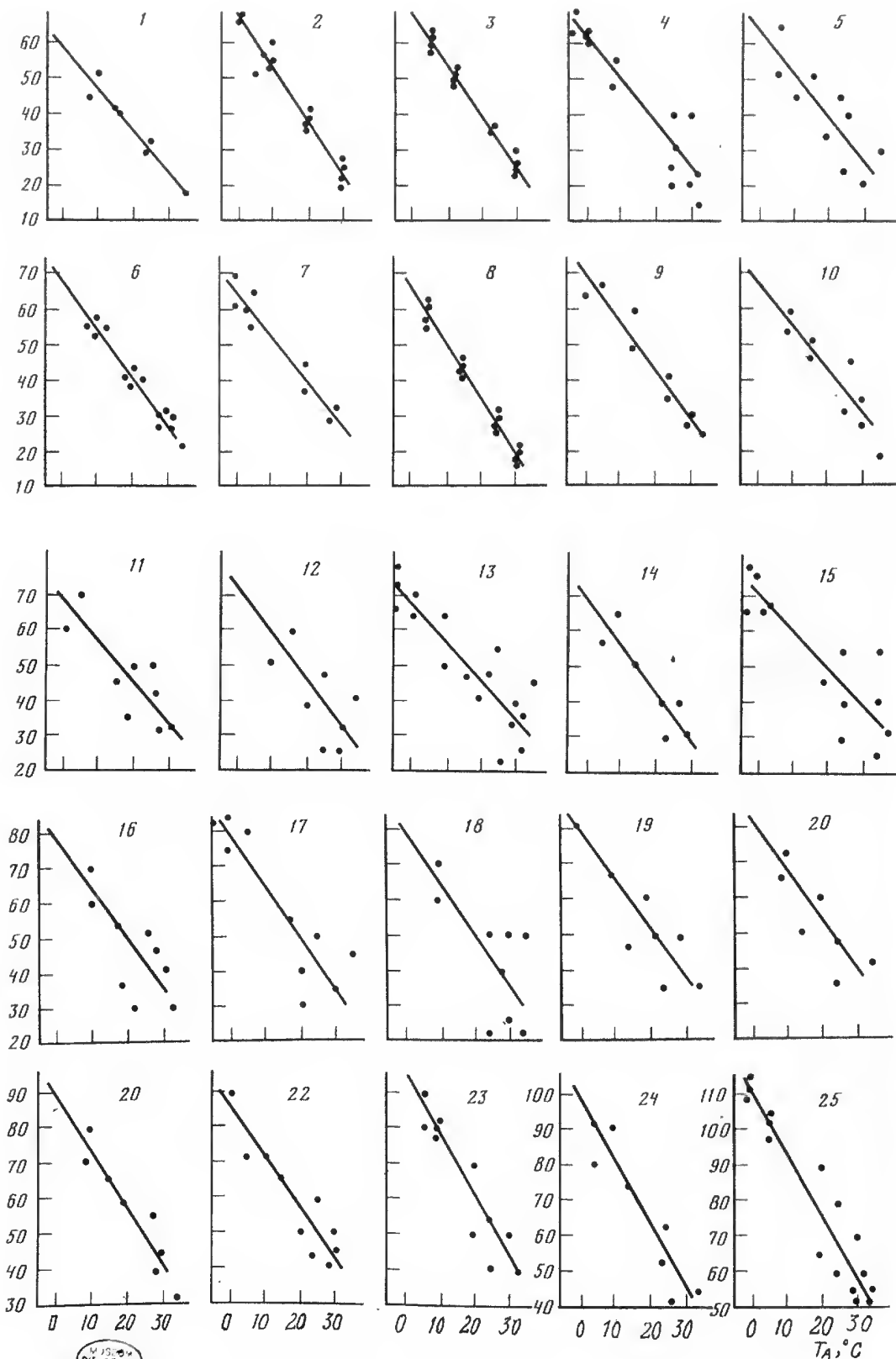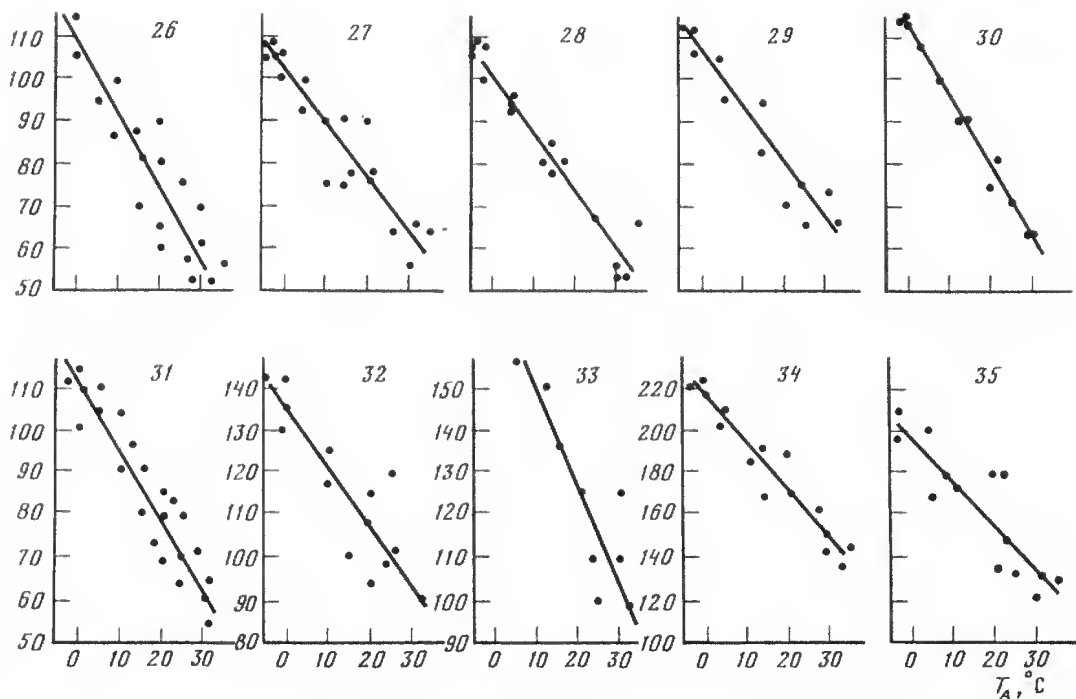
F i g. 1. Relation exiatence energy (ordinata, kJ bird⁻¹ day⁻¹)to ambient
temperatures (absciasa,$T_A$, °C) in summer in passerine birds

1 - Phylloacopus sibilatrix,
2 - Estrilda troglodytes
3 - Tiaris canora
4 - Aegithalos caudatus
5 - Troglodytes troglodytes
6 - Uraeginthus bengalis
7 - Parua ater
8 - Phylloscopus trochilus
9.- Lonchura striata
10 - Sylvia curruca
11 - Parus palustris
12 - Acrocephalus schoenobenus
13 - Spinus spinus
14 - Serinus canaria
15 - Acanthis flammes
16 - Phoenicurua ochruroa
17 - Erithacus rubecula
18 - Hippolais icterina

19 - Motacilla alba
20 - Saxicola rubetrs
21 - Anthus pratensis
22 - Motscilla alba
23 - Sylvia atricapilla
24 - Sylvia nisoria
25 - Carpodacus erythrinua
26 - Passer d. bactrianus
27 - Passer domesticus
28 - Lanius collurio
29 - Chloris chloris
30 - Emberiza hortulana
31 - Emberiza citrinella
32 - Loxia curvirostra
33 - Oriolus oriolua
34 - Turdus philomelos
35 - Turdus merula

Table 3. Gross energy in three species at different diets

| Species | Winter | | Summer | |
|---|---|---|---|---|
| | grain | egg | grain | egg |
| Parus major | 60.3 | 54.0 | 77.5 | 62.4 |
| Fringilla coelebs | 76.2 | 62.8 | 97.1 | 67.8 |
| Nucifraga caryocatactes | 238.2 | 244.1 | 309.8 | – |

Table 4. Relation of bioenergetic parameters to body mass (m)

| | Granivorous | Insectivorous |
|---|---|---|
| Summer | n=9, lim n=12.0–44.7 g | n=20, lim m=7.6–83.0 g |
| $EMR_{0^\circ}$, kJ bird$^{-1}$day$^{-1}$ | $18.6\ m^{0.5434}$ | $19.6\ m^{0.5268}$ |
| $EMR_{30^\circ}$, kJ bird$^{-1}$day$^{-1}$ | $6.1\ m^{0.7221}$ | $5.6 m^{0.7122}$ |
| BMR, kJ bird$^{-1}$day$^{-1}$ | $5.5\ m^{0.5899}$ | $4.2\ m^{0.6358}$ |
| Winter | n=18, lim m=12.0–53.4 g | n=18, lim m=8.8–112.0 g |
| $EMBR_{0^\circ}$, kJ bird$^{-1}$day$^{-1}$ | $20.5\ m^{0.4912}$ | $20.1\ m^{0.5074}$ |
| $EMR_{30^\circ}$, kJ bird$^{-1}$day$^{-1}$ | $6.3\ m^{0.6916}$ | $6.7\ m^{0.6528}$ |
| BMR, kJ bird$^{-1}$day$^{-1}$ | $4.3\ m^{0.6853}$ | $4.8\ m^{0.6234}$ |

ive of the fact that the same values at different seasons (existence energy at 0°C and 30°C; basal metabolism and heat conductivity under normal conditions) are characterized by a specific inderdependence between these indices and body mass both in granivorous and insectivorous. During the other seasons this interdependence changes.

Basal metabolism in insectivorus birds is lower than in granivorous, especially in summer (Table 4, Fig. 2). Energy of existence at 30°C is also higher in granivorous birds (Table 4, Fig. 2), its relationship with basal metabolism being similar in granivorous and insectivorous passerines, but varies seasonally. In summer the energy of existence at 30°C is 1.66 times as high as that of basal metabolism rate both in insectivorous and granivorous, and in winter 1.51 and 1.53 times, respectively.

The energy of existence at 30°C in winter is practically similar in insectivorous and granivorous birds, but in summer it is higher in insectivorous species, suggesting that cold conditions are much less favourable for insectivorous birds, especially in summer.

If basal metabolism is a peculiar measure of power(Benett, Ruben, 1979) and the general amount of energy expended invariably increases proportionately to the basal, and by an equal number of times, these data indicate that granivorous species have greater existence power, and under cold conditions have a greater safety margin.
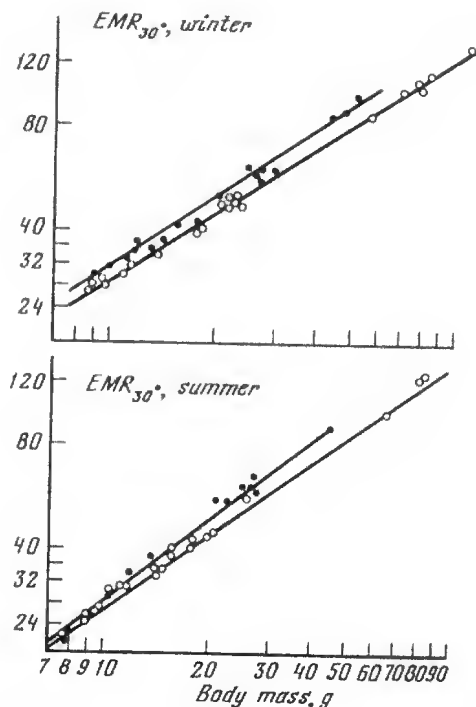
F i g. 2. Relation between existence energy at 30 (ordinata, kJ bird$^{-1}$day$^{-1}$) to body mass in winter (above) and summer (lower) in insectivorous (white circles) and granivorous (dark circles) passerines birds

Energy requirements of a granivorous passerine for existence, as well as various types of activity, are greater in comparison with an insectivorous one. Consequently, granivorous birds consume a disproportionally large amount of food and exert an appreciably greater impact on lower trophic levels compared with other organisms of similar size (the metabolic rate of passerines is higher than in all other animals).

Thus, there is a reason to believe that adjustment to granivory provides passerines with a greater energy flow and they have a good deal of power, which can be additionally enhanced, for other types of activity and thermoregulation under a cold stress. Granivory is an ecological niche with a great energy flow.

References

Benett A.F., Ruben J.A. - Science,1979, 206, N 4419.

Dolnik V.R., Gavrilov V.M. - In: Ecologitcheskie i fisiologitcheskie aspekty pereletov ptits. Leningrad, Nauka, 1971, p. 226-235.

Gavrilov V.M. - Zool. Zurn., 1979, 58, N 4, 5, p. 530-541, 693-704.

Gavrilov V.M. - In: Ecologia, geographia i okhrana ptits. Leningrad, 1980a, p. 73-97.

Gavrilov V.M. - Ornitologia, 1980, N 15, Moscow, p. 208-210.

Gavrilov V.M. - Ornitologia, 1982, N 17.

## ON STRUCTURE OF BLACK-HEADED GULLS (LARUS RIDIBUNDUS) COLONIES

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It was studied the way of some black-headed gulls shift their territories inside the colony during a breeding season. In the very beginning of the seasons of 1980 and 1981 106 and 112 gulls were stained with different colours and wing-tagged at the same time. These marked birds resettlements were observed. In 1982 300 gulls that had been wing-tagged in previous years were observed.

From 30 to 71 per sent of the gulls which territories were in peripheral or in pericentral parts made attempts to resettle and occupy a territory in the centre. On the average 23% of the gulls managed to do it. Some of the abandoned places were occupied by the new arrivals, some remained vacant. Thus, throughout a breeding season these is a pronounced centripetal stream of the resettling individuals in the colony of black-headed gulls (Fig.1, 2).

On the average 7% of gulls resettled from the centre to pericentre. In 1982 isolated cases of resettlements from the centre to peripheral parts were observed. Thus, a centripetal stream is much more expressed than a centrifugal one. The latter may possibly be explained by a strong competition in gaining territories in the centre of colony.

The observations were carried out in the colony of black-headed gulls on the Kiyovo lake (Moscow region) in the springs of 1980, 1981 and 1982. The colony had: 1980 - 15400 breeding pairs, 1981 - 15000 b.p. and 1982 - 16500 breeding pairs. The functional centre, the pericentre and the peripheral
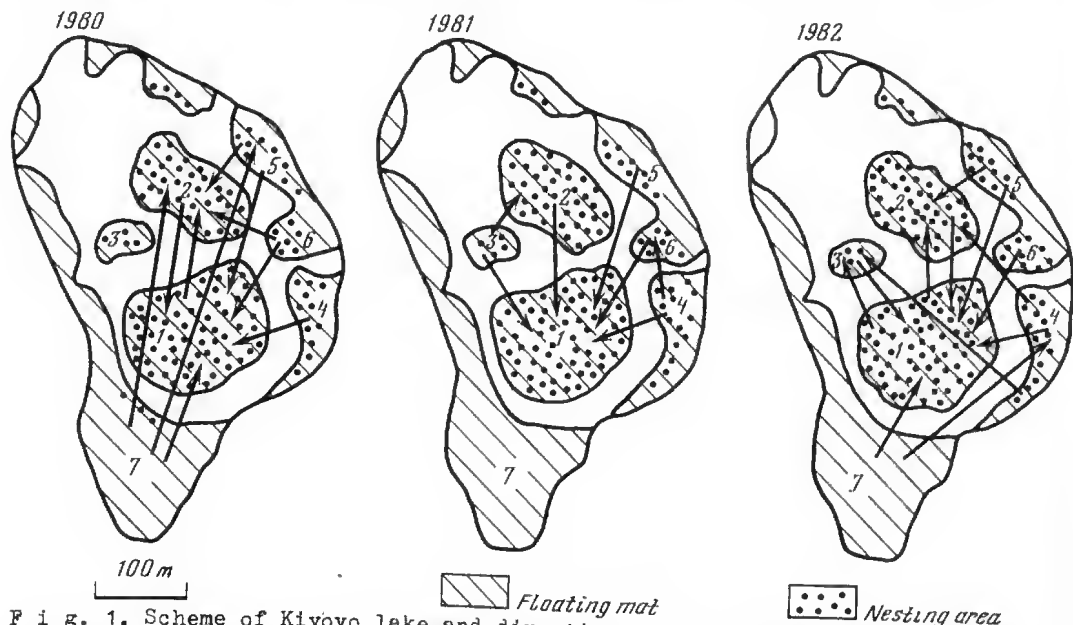


Fig. 1. Scheme of Kiyovo lake and directions of the Black-Headed Gulls observed resettlements (arrows) in seasons of 1980, 1981 and 1982
1 - centre; 2 - pericentre; 3-7 - peripheral parts and edge of the colony

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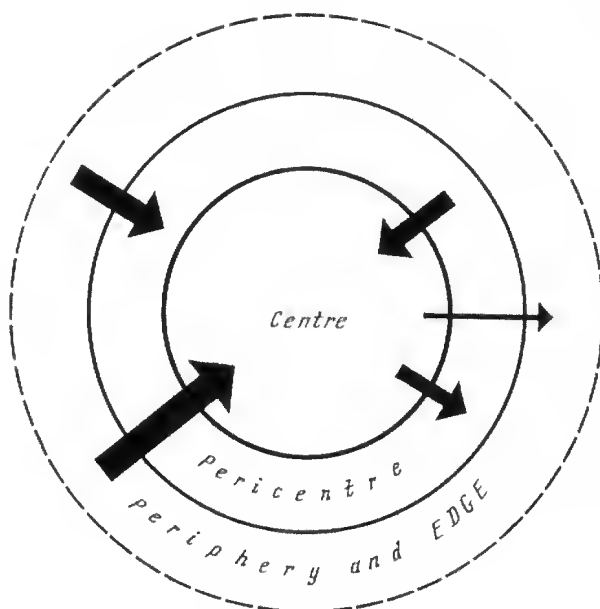
F i g. 2.Scheme of the Black-Headed Gulls colony and directions of their re-settlements inside the colony throughout a breeding season. The arrows thick-ness reflects the number of resettlements

parts of this colony have been separated from one another spatially and si-tuated on different floating mats. The first gulls that arrive from their wintering grounds always settle in the future centre of the colony. Then all the colony area becomes occupied in 2-3 days, but the density of gulls po-pulation is low. Further on the density is increasing since the new arrivals intrude into the colony. The number of intrusions to occupy some territory increases from the edges to the centre of the colony $(h^2=46.9\%;$ n=28; f=30.2; p < 0.001; see Table).

The number of intruders in a twenty chosen gulls flying over the different parts of the colony

| Date of the observation | The number of intruders | | |
|---|---|---|---|
| | over the centre | over the pericentral parts | over the peripheral parts |
| 10.4.80 | 3 | not counted | 1 |
| 11.4.80 | 3 | 1 | 2 |
| 12.4.80 | 5 | 4 | 1 |
| 16.4.80 | 3 | .4 | 1 |
| 21.4.80 | 9 | 4 | 3 |
| 26.4.80 | 10 | 9 | 4 |
| 27.4.80 | 9 | 6 | 2 |
| 27.4.79 | 9 | not counted | 1 |
| 29.4.80 | 10 | 2 | 0 |
| 1.5.80 | 10 | 3 | 0 |

SOUND IMITATION IN THE FORMATION OF COMMUNICATION
BETWEEN MAN AND BIRDS

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Folk and onomatopoeic names of birds. The method of biolinguistic inter-
lingual parallelisms (Dementiev, Ilyichev, 1963) was used to study the folk
names of 8 species of birds based on sound imitation in 10-40 Indo-European,
Finno-Ugric and Turkic languages.

The diachronous formation of onomatopoeic names based on the first imitat-
ing reflexes of man is a part of the process of using environmental sounds by
man to form his own accoustic behavior (music, sound imitating names, inter-
jectory vocabulary of communication with animals).

As a result of acoustic comparison of onomatopoeic names and their corre-
lates in the signalization of birds[*] by means of sound analysing instruments
it was found that:

1. In a onomatopoeic name consisting of three syllables the initial fre-
quency maximums are approximately in the same ranges as in birds' call.

2. The intervals between the syllables in a bird's call correspond to
those of the name uttered by man.

3. The amplitude characteristics of a bird's call also correspond to
those of a "human" signal.

4. The initial and terminal energetic maximums are transfered from a
bird's voice into an onomatopoeic name.

Ecologo-acoustic studies suggested that in most cases the imitation of
contact calls of birds served as a basis for the formation of onomatopoeic
names.

A biolinguistic comparison of Russian and Bashkir folk names of birds as
well as ecological analysis of onomatopoeic names of the Bashkir language
showed that:

1. Of 235 species of birds in the fauna of the Bashkir ASSR and the South
Urals 113 names are associated with birds' voices, moreover, the names of 84
species are only onomatopoeic without non-onomatopoeic synonims. Some species
have from 2 to 7  onomatopoeic synonims.

2. The principle of nominating a species by voice in Russian and Bashkir
names coincides for 37 species (30%). Ten biolinguistic parallelisms were
found among them.

3. The greatest number of onomatopoeic names in the Bashkir language is
found among water fowl (45%), forest and bush birds come next and then the
names of open space birds. Predators account for the smallest number of
onomatopoeic names in the Bashkir language (the names of only 5 species of
25 are onomatopoeic).

4. The ecologically related character in the nomination of birds is es-
pecially pronounced in the Bashkir language.

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[*] The attracting call of Cuculus canorus and its species name in Russian
"kukushka" (cockoo) were analyzed.

<u>Man-bird bioacoustic contacts</u>. Attracting and repellent signals based on onomatopoeia which had appeared during domestication of wild animals were ascertained. These signals gradually enriched the vocabulary of various languages. The similarity of such lexical attractants and repellents transformed by man was noted in the languages of various linguistic groups.

Biolinguistic analysis was used to ascertain interlingual parallelisms (in 9 languages) of the most ancient lexical repellent "kysh" (Russian), "ksch" (German). Its role as a conglomerate of defense signals not only of birds but also of other animals was shown.

The role of acoustic communication based on sound imitation between man and birds ("speaking" in particular) was evaluated in the creation of signal-orienting medium necessary for ethological comfort of caged birds. The ability of birds to imitate human speech is regarded as an effective means for controlling the behavior of birds.

The bird's voice formed on the basic of nature acoustic medium participates it self in the formation of the acoustic medium of the man.


Scheme shows the interinfluence between the bird's voice and the acoustic medium (nature sounds and sounds of humen origin):

| Noises of inanimate nature and vegetation | Sounds connected with human activities | Human speech and music | Animals and birds voices |
| --- | --- | --- | --- |

bird's voice

Imitation by human voice
↓
Imitation by human voice and/or decoy-device
↓
Acoustic repellents

Onomatopoeic names

Onomatopoeic melodies for the voice
↓
Onomatopoeic melodies for musical instruments
↓
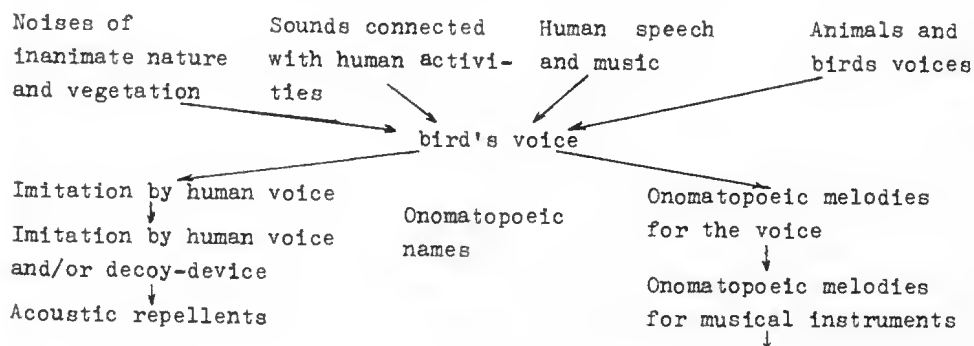
R e f e r e n c e s

Dementiev G.P., Ilyichev V.D. - Ornithologia, 1963, N 6, p. 401-407.

Ilyichev V.D., Silajewa O.L., Tikhonov A.V. - Ornitologia, 1983, N 18, p. 156-162.

Ilyichev V.D., Silajewa O. - In: Zvukovaya sreda kak stimuliruyusthyi i vozdeistvuyustchyi faktor. Moscow, 1985, p. 217-226.

Ishberdin E.F., Silajewa O.L. - In: Zvukovaya sreda kak stimuliruyustchyi i vozdeistvuyustchyi faktor. Moscow, 1985, p. 226-236.

Silajewa O.L. - Ornitologia, 1981, N 16, p. 183-185.

Silajewa O.L. - Der Falke, 1981, H. 12, S. 408-413.

Silajewa O.L. - Ornithologia, 1982, N 17, p. 189-191.

TAXONOMIC STATUS AND HISTORICAL FORMATION
OF THE AREA OF COMMON SWALLOWS (HIRUNDO RUSTICA)
IN THE AMUR REGION

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Our collections and observations made in various localities of the Amur
river region in 1970-1980 involving other extensive collection material ser-
ved as a basis to show that common swallows of the Amur region occupy the
intermediate position between the two Asiatic subspecies Hirundo rustica tyt-
leri Gerd. (Baikal region) and H.r.gutturalis Scop. (Far East Maritime reg-
ion and China). The polymorphism of these birds resulted from hybridization
of the given subspecies which had long been separated by the territory with
no places suitable for nesting. The appearance of common swallows in the
Amur region coincide with the beginning development of this region by new
settlers from Russia in the 17th century and stem from the emergence of
structures suitable for nesting. The use of size features and ascertained
coloration types makes it possible to clearly identify the subspecies of
H.rustica in their time under field conditions. This is particularly import-
ant for the identification of migratory, flown in and wintering birds as
well as for fixing the dynamics of subspecies areas.

Common swallows occur in the Northern hemisphere from deserts to forest
tundra. They inhabit North Africa, Europe, Asia,North America. Their synant-
ropy (almost everywhere the birds nest on man-made structures) and food spe-
cialization (they feed mostly on small flying insects) account, on the one
hand, for a wide distribution of the species and, on the other hand, an ex-
tremely irregular distribution of the birds inside the area. This species
reaches the greatest numbers in livestock breeding regions with plenty of
food and places suitable for nesting. The common swallow is characterized by
a great geographic variability of coloration and size. Certain geographic
populations are also polymorphous in a number of features.

The Amur region is completely incorporated in the nesting area of the
species, however the birds are numerous only in populated agricultural reg-
ions. Common swallows nest here only on man-made structures, and in localit-
ies remote from them only migratory and non-nesting individuals can be found.
In the heart of taiga and along mountain ranges these birds can hardly be
found at all. The climatic conditions on the coasts of  Okhotsk  Sea
and Gulf of Tatary are unfavorable for them.

To define the taxonomic status of the birds inhabiting the Amur region,we
carried out observations and collected material in various localities of the
entire territory in 1970-1980 , 112 specimens  of the birds  were ob-
tained and 79 of them were investigated in their life time. We studied the
material for other regions from the collections of the Zoological Institute
of the USSR Academy of Sciences(Leningrad), the Zoological Institute of the
Ukranian SSR Academy of Sciences(Kiev), Zoological Museum, Biological and
Geographical departments of the Moscow State University, Biological depart-
ment of the Kiev University. We are greatly indebted to the research workers
of the indicated institutions, to S.V.Vinter who offered 12 specimens of

Size features of common swallows of the Baikal region,
Amur region and Far East Southern
Maritime territory[*]

| Region | Sex | Wing length | | | | |
|---|---|---|---|---|---|---|
| | | Lim | M | $\sigma$ | $\overline{M}$ | n |
| Baikal | ♂♂ | 114.0–125.0 | 117.7 | 3.12 | 116.66–118.74 | 37 |
| | ♀♀ | 105.2–123.8 | 116.3 | 3.61 | 115.11–117.49 | 38 |
| Amur | ♂♂ | 106.0–118.0 | 112.7 | 3.22 | 111.79–113.21 | 80 |
| | ♀♀ | 103.5–118.5 | 111.3 | 2.85 | 110.66–111.94 | 79 |
| Far East Southern Maritime | ♂♂ | 105.5–119.0 | 112.6 | 3.17 | 111.63–113.37 | 53 |
| | ♀♀ | 104.0–117.0 | 110.1 | 3.18 | 108.95–110.25 | 31 |

| Region | Sex | Length of extreme rectrices | | | | | Relative length of tail |
|---|---|---|---|---|---|---|---|
| | | Lim | x | $\sigma$ | D | n | |
| Baikal | ♂♂ | 82.5–123.5 | 103.1 | 9.46 | 99.68–106.52 | 32 | 0.88 |
| | ♀♀ | 80.0–113.0 | 90.9 | 6.78 | 88.61–93.19 | 36 | 0.78 |
| Amur | ♂♂ | 82.5–119.0 | 100.0 | 8.53 | 98.10–101.90 | 80 | 0.89 |
| | ♀♀ | 71.5–96.6 | 83.9 | 4.85 | 82.81–84.89 | 79 | 0.75 |
| Far East Southern Maritime | ♂♂ | 80.0–116.5 | 96.0 | 8.60 | 93.60–98.40 | 52 | 0.85 |
| | ♀♀ | 63.0–90.0 | 80.9 | 5.34 | 78.91–82.89 | 30 | 0.73 |

[*] Common swallows from the Baikal region and Far East Southern
Maritime territory differ significantly in the length of the
wing, extreme rectrices and relative length of the tail

birds from the Central Amur region, to N.D. Poyarkov handed over at our dis-
posal 2 specimens of birds from Lake Chukchagir, as well as to R.L. Böhme,
N.N. Kartashev and A.A. Kishchinsky for their useful advice on the given ar-
ticle.

ANALYSIS OF TAXONOMIC FEATURES

All the subspecies of common swallows are characterized by a certain variability of features, however' only the tail length has its individual (apparently age-related) changeability. Common swallows from the Amur region seem to stand spart in this respect. Even among the few birds obtained here by the beginning of the 1970s there are individuals both similar and dissimilar in size and coloration. The situation is complicated by the fact that the places where the birds with palely- and dark-ocherous lower part of the body were captured are distributed in a mozaic pattern throughout the entire territory; in some cases birds with different coloration were found in the same district (Stegmann, 1931; Spangenberg, 1940). The incompleteness and diversity of the material were responsible for contradictory evaluations of the taxonomic status of these birds (Hartert, 1910; Buturlin, Dementiev, 1937; Portenko, 1954; Vaurie, 1959; Stepanyan, 1978). Each author determined the number and composition of subspecies (from two to four) and the boundaries of their distribution in the Amur region in his own way.

Size features. The study on birds' variability included: the length of the wing, the extreme and middle rectrices (from the site where the feather comes out of the skin to its tip, of the metatarsal bone, bill (from the nostril and from the forehead plummage to the bill tip), the width and height of the bill at the nostril, the tail to wing length ratio. Due to lack of material for birds from the Baikal region, Far East Maritime territory and China we failed to compare such indices as the weight and the total body length of the birds. This also explains the fact that while calculating the tail index we related the tail length to the wing length, though for remote migrants the comparison of the tail length with the total body length yields more reliable results.

It was found that the birds from various places of the area do not differ significantly in the length of the middle rectrices, metatarsal bone, bill, in the width and height of the bill. The birds from the Baikal region and Far East Southern Maritime territory (both males and females) differ significantly(P=0.95)  from each other in the length of the wing and extreme rectrices as well as in the tail index, the birds from the Baikal region being greater in size. Common swallows from the Amur region as a whole occupy the intermediate position between the birds from the Baikal region and Far East Southern Maritime territory (see Table; Fig. 1a,b).There are no significant differences between males from the Amur region and the Baikal region in the length of extreme rectices, at the same time no differences are found between males and females from the Amur region and Far East Southern Maritime territory. The females occupy the intermediate position in relative length, while the males from the Amur region are superior to the birds from the Far East Southern territory and Baikal region.

Coloration. A study was made on the variability in the coloration of the lower and upper parts of the body, neck, forehead, spots on the rectrices,
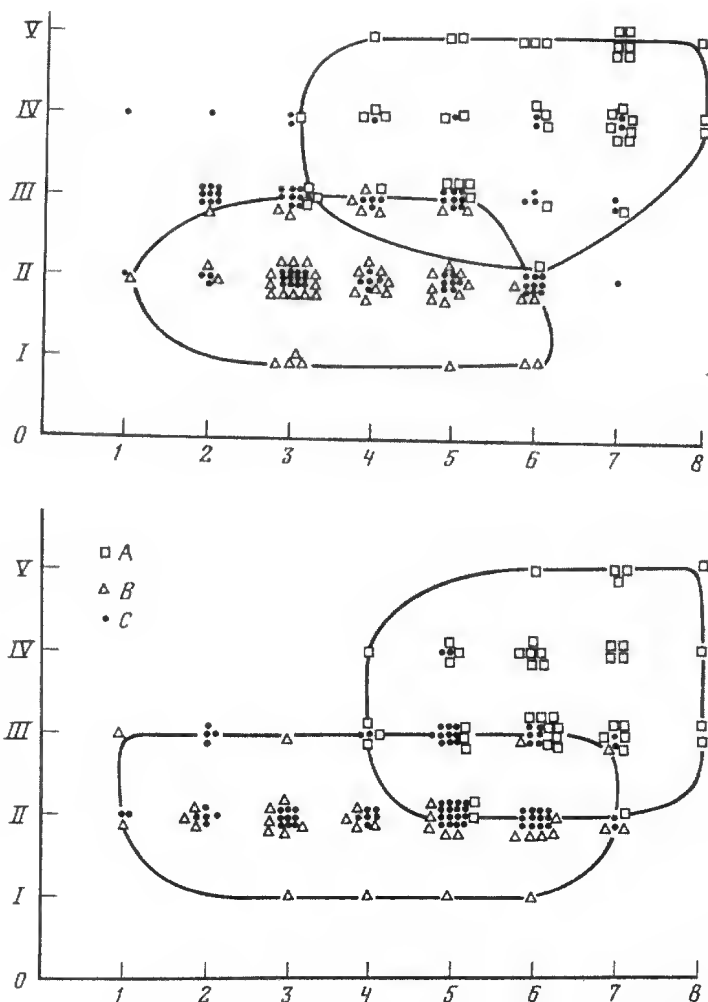
F i g. 1. Diagram of variability in the length of the wing (a) and extreme rectrices (b) of common swallows in the Baikal Region (A), Amur region (B) and Far East Southern Maritime territory (C): vertical section - total amplitude of variability; wide stripe - 2; light rectangle - M (confidence limits of general mean; transverse section - M (mean value)

transverse stripe on the breast. It was found that the coloration of the abdomen, forehead, neck, spots on the rectrices had individual variability and in general correlated well with the coloration of the lower part of the body. We found no significant geographic differences in the coloration of the upper part of the body.

The coloration of the lower part of the body in common swallows within their area is characterized by a wide variability which is hard to describe

verbally. The wide diversity of ocherous shades is impossible to define even by Bondartsev's scale (1954). Examination of the collections (more than 600 specimens) showed that the common swallow inhabiting the USSR territory may be visually distinguished into 16 groups by color intensity of the lower part of the body. Further analysis showed that such detailed description was unnecessary, and the definition can be confined without any deterioration in determination to the following five main types: 1) pure white; 2) palely-ocherous; 3) light-ocherous; 4) ocherous; 5) dark-ocherous. With some skill. it is possible to distinguish precisely the coloration type in nature without comparing with collection specimens.

Analysis showed that within the boundaries of every geographic region the coloration of the lower part of the body varied to a small extent. At the same time, birds from the Baikal region and Far East Southern Maritime territory (both males and females) differ significantly (P = 0.95) from each other in this feature. Birds from the Baikal region lack the first coloration type, while those from Far East Southern territory - the fourth and fifth coloration types of the lower part of the body. Moreover, the males from the Baikal region show the predominance in the fourth and fifth coloration types, and the males from the Southern Maritime territory - the second type. The birds from the Amur region occupy the intermediate position in this feature. They are characterized by the second-fourth coloration types noted for all the colonies investigated. The coloration of the lower part of the body in the males and females making up a pair may be similar or different. The coloration of young birds is duller, but their individual differences within a colony are as great as in adult birds.

The transverse stripe on the breast is observed in most common swallows: ocherous feathers on the neck and the plummage on the breast are separated from each other by a stripe of black feathers. Frequently among black feathers of the transverse stripe there are some feathers or groups of feathers partly or completely ocherous; these feathers are similar in intensity to those of the neck. In some birds the black feathers of the transverse stripe are retained only on the body flanks. The descriptions of the transverse stripe previously employed (continous, interrupted, etc.) had not reflected the whole extent of its variability and precluded an objective evaluation of this feature. In order to describe the diversity in the structure of the transverse stripe as completely and as objectively as possible, a scheme was made up (Fig. 2). The coloration types were distinguished by the intensity in the development of ocherous feathering. The reference of one or two variants (a, b) to one type is associated with difficulty of their discrimination when the distal part of a feather has two colors (black and ocherous).

It was found that within the boundaries of each region this feature has little variability. Common swallows from the Baikal region and Far East Southern Maritime territory differ from each other in this trait (P = 0.95). The males from the Baikal region are found to have the third-eighth types (fifth-seventh are predominant), the males from the Far East Southern Maritime territory have the first-fifth types (third-fifth are predominant). The transverse stripe among the females of the Baikal region is of the fourth-
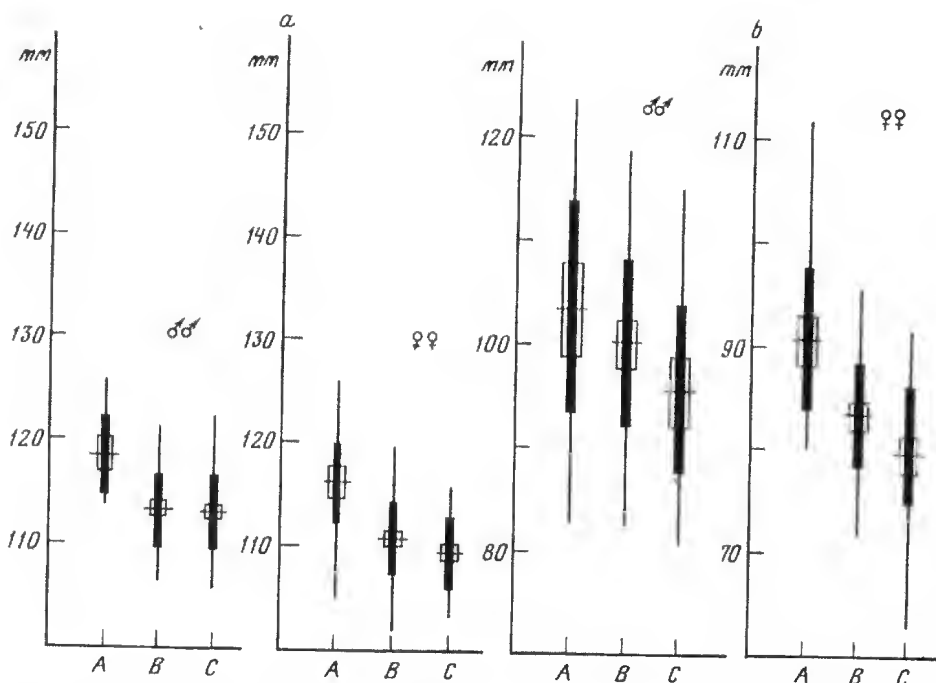
F i g. 2. Structure of the transverse stripe on the breast; 1-8 - tipes of transverse stripes; b - type variants

eighth types (fifth-seventh are predominant), and among the females from the Far East Southern Martime territory it is of the first-seventh types (third-sixth are predominant). Common swallows from the Amur region occupy the intermediate position by this index. They lack the eight type of the transverse stripe, while both males and females show the predominance of the second-sixth types. This pattern was observed in all the colonies investigated. The structure of the transverse stripe in males and females making up pairs is usually different. The young birds from one colony also differ in this index.

Simultaneous comparison of two indices (structure of the transverse stripe and the coloration of the lower part of the body) in common swallows from the Baikal, Amur and Southern Maritime regions reveals even more distinctly the intermediate position of the birds from the Amur region (Fig. 3)[*].

Thus, all the colonies investigated are characterized by polymorphism. No clinal variability within the investigated territory of the Amur region was ascertained. All the colonies were found to have birds, the features of which were characteristic of both Hirundo rustica.tytleri Gerd., inhabiting the Baikal region, and H.r.gutturalis Scop., inhabiting the south of the Far East Maritime territory and China. All this confirms Stegmann's opinion (1931) that the Amur region is a transitional zone between H.r. tytleri and H.r.gutturalis. Therefore, there are no grounds for including the Amur region in the area of H.r.rustica, H.r.tytleri, H.r.gutturalis, or refer the swallows of the Amur region to H.r.erythrogaster.

F i g. 3. Variations in the coloration of the lower part of the body and
the transverse stripe on the breast of common swallows in the Baikal region
(A), Amur region (B) and Far East Southern Maritime territory (C): I-V –
coloration types of the lower part of the body, 1-8 – types of the trans-
verse stripe on the breast; upper – males, lower – females

COLONIZATION OF THE AMUR REGION
BY COMMON SWALLOWS

When establishing the taxonomic status of common swallows from the Amur
region, the biological features of this species were not taken into account
and the distribution of subspecies of common swallows in the south of the
Far East and their interrelations were regarded as static. Colonization of
this territory is believed to coincide with the period following the last
glaciation (Stegmann, 1929). However, a rise in temperature is the neces-
sary, but not the only condition of habitation of common swallows. As men-
tioned above, almost everywhere the birds nest only on man-made structures
and feed mainly on small  flying insects. The colonies of common swallows

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\* The use of size features, coloration types of the body's lower part and
the structure of the transverse stripe makes it possible to identify
precisely to what subspecies the given common swallow belong under field
conditions in its life time. This is particularly important for identifi-
cation of migratory, flown in and wintering birds, as well as for fixing
the dynamics of subspecific areas. Incorporation of data on the weight
and body length will enhance the precision of their identification.

are especially numerous on livestock farms. The birds procure their food near grazing animals, where "air plankton" is concentrated.

The close relation of common swallows with herbs of ungulate animals is attested by the fact that an increase in the size of farms leads to a greater number of nests in the colonies. Other conditions being equal, the size of colonies in barns with livestock is greater than in empty barns. For instance, in Razdolnoe village (Far East Maritime region) in the barns where calves were kept there were 27 nests with swallows, while in the neighboring barns, from where the calves were taken to summer pastures, none of the 32 nests were occupied by the birds. A similar situation was observed in other districts of the southern Far East. Apparently, this is explained by a more favorable microclimate of habitable places and by the abundance inside such structures of insects which are active throughout the year. This accounts for unusual cases of wintering of common swallows in a large cow barn in the village of Russkaya Polyana (Khabarovsk region), of which we were informed by local residents. Wintering swallows were observed on farms in the Amur region (Efremov, Pankin, 1975).

Permanent settlements and the first rudiments of producing households of people populating the Amur region began to emerge as far back as the stone age. However, up to the 20th century their main occupations were hunting and fishing; this was largely responsible for a low total population and their confinement  to large rivers and lakes. Even in large settlements the dwellings were of the underground type (Okladnikov, Derevyanko, 1973) unsuitable for nesting of common swallows. In 1664 the first Russian explorers headed by Vasily Poyarkov reached the Amur river. This marked the beginning in the colonization of this territory, which became particularly intensive from the middle of the 19th century. Up to the 19th century the territory of neighboring Manchuria also remained sparsely populated. In 1850 the population of the Amur district reached 10,000, by the beginning of the 20th century - 50,000. The population growth became particularly rapid beginning from the 30s of the present century(Sychyovsky, Sapunov, 1974).

Taking into consideration  a number of biological features of common swallows, it may be assumed that they started to nest in the Amur region. with the emergence of the first Russian settlements. This is testified by the following: 1) the birds are regularly found in summer in regions unsuitable for nesting (the lower part of the Ob river, Taimyr, New Siberian Islands, Chukotsk Peninsula); 2) the appearance of the first, even temporary structures in regions uncolonized by the species as well as that of domestic animals leads to an immediate colonization of the new territories by common swallows. For example, in Sakhalin the first common swallows were found to nest in 1923 immediately after a fur farm and fish cutting facilities had been built (Yamashina, 1931); 3) the birds colonize new structures in the first summer. In the Amur region we saw no swallows during the nesting period far from populated areas, but near a tent or  a car the birds appeared the next day.

Colonization of the Amur region by common swallows seems to have proceeded from different sides and reflected the successive emergence of populated areas on this territory. Common swallows from the Amur region are characterized by polymorphism and intermediate (as regards <u>H.r.tytleri</u> and <u>H.r. gut-</u>
1239

turalis) features. The birds from the Uda river make up an exception. All the six specimens obtained here in 1844-1845 by the expedition headed by A.T.Middendorf and a male obtained in 1914 have dark-ocherous coloration (fifth type) of the lower part of the body and the seventh-eighth type of the transverse stripe. Middendorf (1867) specially emphasized that he had encountered birds here having a dark lower part. In our opinion, this provides evidence for the fact that by the beginning of the 20th century the northern parts of the Amur region had been colonized only by H.r.tytleri, whereas the penetration of H.r.gutturalis and hybridization of these subspecies here started later on.

It is rather hard to map the territory inhabited by the hybrid form. This is due to not only irregular exploration of the Amur region and adjacent territories, but also to incomplete hybridization of the two subspecies. Thus, the north of the Far East Maritime region and the south of the Khabarovsk region to the west of Sikhote Alin, which were unanimously included in the area of H.r.gutturalis, as well as the north of the Amur region,where H.r.tytleri initialy penetrated, are inhabited now by the hybrids.

In conclusion we would like to consider a possible influence of H.r.erythrogaster on the birds of the Amur region. The common swallow is a day migrant and the migratory and feeding activity of this species coincide with each other (Lyuleyeva, 1971). The daily migrations of this species are not long, therefore the possibility of common swallows to cross extensive water spaces of the Pacific is very small. The American and Asiatic subspecies show dissociation not only in nesting areas but also in wintering areas and migratory routes. Common swallows widely occur in the south of the Far East and of North America, but no migrations between these regions have been observed. According to studies involving banding (Lebedeva, 1968), the birds nesting in the Amur region winter together with those from the Baikal region, Far East Southern Maritime territory and China in the South East Asia. A few birds which occasionally cross the Pacific can not influence substantially the continental subspecies and their descendents should acquire the appearance of the native subspecies, as shown for other classes of vertebrates. The polymorphism of common swallows in the Amur region resulted from the allopatric hybridization of the two Asiatic subspecies which has been separated by the territory for a long time, where there were no places suitable for nesting.

SUMMARY

Polimorfism of these birds is the result of allopatric hybridization of the swallows from Transbaikalia and China separated for a long time by a territory hatching in places suitable for nesting. The appearence of the Barn Swallows in the Amur territory and the hybridisation of subspecies are due to the appearance of dwellings made by immigrants from Russia in the 17th century. The use of meristic characters and types of collor allows to identify precisely the subspecies of the Hirundo rustica vitally in the field conditions, which is especially important for the identification of migrant, vagrant and wintering birds and the fixation of dynamics of the subspecies ranges.

R e f e r e n c e s

Bondartsev A.S. Coloration scale. A manual for biologists for scientific and science applied investigations. Moscow; Leningrad: USSR Acad. Sci. Publ., 1954, p. 1-27.

Buturlin S.A., Dementiev G.P. Polnyi opredelitel ptits SSSR. Moscow: KOGIZ, 1937, 4, p. 1-334.

Efremov V.F., Pankin N.S. - In: Zhivotnyi mir Dalnego Vostoka. Blagoveshchensk, 1975, 3, p. 58-63.

Lebedeva M.I. - In: Ornitologiya. Moscow, 1968, N 9, p. 270-276.

Lyuleyeva D.S. - In: Ekologicheskie i fiziologicheskie aspekty perelyotov ptits. Trudy Zoologicheskogo Instituta Akademii Nauk SSR. Leningrad, 1971, 50, p. 183-225.

Okladnikov A.P., Derevyanko A.P. Dalyokoe proshloe Primorya i Priamurya. Vladivostok: Dalnevostochnoe knizhnoe izdatelstvo, 1973, p. 1-140.

Portenko L.A. Ptitsy SSR. Part 3. Moscow; Leningrad: USSR Acad. Sci. Publ., 1954, p. 1-325.

Spangenberg E.P. - In: Trudy Moskovskogo zooparka. Moscow, 1940, 1, p. 77-136.

Stepanyan L.S.  Sostav i raspredelenie ptits fauny SSSR. Vorobinoobraznye. Passeriformes. Moscow: Nauka, 1978, p. 1-391.

Sychevsky E.P., Sapunov B.S. - In: Amurskaya oblast. Blagoveshchensk, 1974, p. 357-459.

Shvarts S.S. Ekologicheskie  zakonomernosti evolutsii. Moscow: Nauka, 1980, p. 1-278.

Hartert E. Die Vögel der paläarktischen Fauna. B., 1910, 1, p. 832.

Middendorff A.Th. Sibirische Reise. Säugethiere, Vögel und Amphibien, 1867, 2, p. 1-256.

Stegmann B.K. - In: Ezhegodnik Zoologicheskogo muzeya Akademii Nauk SSSR, 29. Leningrad, 1939, p. 83-242; J. Ornithol., 1931, 79, N 2, p. 137-236.

Vaurie Ch. The birds of the Pacific Fauna. Passeriformes. L., 1959, p. 7-762.

Yamashina J. - J. Ornithol., 1931, 79, N 4, p. 491-541.

THE GEOGRAPHICAL CORRELATION OF MORPHISM
PHENOMENA IN BIRDS IN CENTRAL ASIA
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The phenomenon of morphism, widely distributed in the class of birds ma-
nifests itself in a wide range of phenotype aspects. As was demonstrated in
the relatively recent survey by Huxley (1955), this problem deserves close
attention since morphism manifestation which are genetically determined,are
associated with major adaptive properties of the organism. The latter ex-
plains their general significance in the evolutionary process.

As a phenomenon of balanced genetic polymorphism, morphism in birds in-
volves a variety of phenotypic aspects, ranging from morphological to eco-
physiological features and behavioural responses. It is currently though
that all its manifestations are based on the same genetic mechanism. But
the outward manifestations of morphism are so diversified that morphism
studies are necessarily differentiated.

One can see from the above-mentioned survey by Huxley, and also from the
practice of ornithological research, that one of the forms of morphism which
immediately meets the eye and whose functional significance is still obscure,
is discrete balanced genetic polymorphism of plumage coloration. The present
paper is concerned with this form of morphism alone.

The Palearctic avifauna provides some examples, which well illustrate the
above phenomenon. Among them, polymorphous populations of Accipiter gentilis,
Falco rusticolus, Oenanthe picata, Oenanthe hispanica, Terpsiphone paradisi
and some other have been studied in detail.

The geographical variability of morphism manifestation is noteworthy. Ac-
cording to Huxley, it is this aspect that should receive particular atten-
tion at the initial stages of investigating the entire phenomenon. The study
of the external patterns of quantitative ratios of morphs in space is in
fact an important starting point of such studies. It is well known that
within the population species systems, some species are characterized by
coloration morphism while others are not. Populations characterized by co-
loration morphism are also differentiated in terms of a degree of its mani-
festation. Thus, it can be inferred that within a species population and,
hence, species range, the phenomenon of morphism is not infrequently record-
ed only in a portion of the population confined to a definite part of the
range. The above is not a rule but a most common pattern. There are only few
species characterized by morphism at the level of the entire species popu-
lation, with the level of its manifestation not varying in space. The geog-
raphical aspect is undoubtedly an important feature of the entire phenomen-
on concerned. Its study will undoubtedly throw light on the problem.

The spatial variability of morphism with special reference to some par-
ticular species has been studied fairly well. For instance, within the range
of Oenanthe picata, three colour morphs have displayed such a rigid distri-
bution pattern, each dominating within its distribution range to such an ex-
tent, that it gives grounds for a taxonomic interpretation of the entire

situation. A population with an almost absolute dominance of a single morph is in good agreement with the subspecies concept taxonomically. Other species show a different pattern. Within the boreal zone of Eurasia, a gradual eastward quantitative increment in the proportion of white morph in the populations of Falco rusticolus is well known. Its maximum incidence (about 50%) of the population occurs at the extreme northeast of the continent. Similarly, the northeast of Asia is the region of maximum incidence of morphism in Accipiter gentilis. It is exactly in the populations of this species that white morph is represented (also about 50%) of the population), which is absent throughout the entire species distribution range. This is the best-known case in the avifauna of Palearctic when spatial localization of parallel morphs coincides (white in the case concerned) in two different species that ever received attention (Dementiev, 1951). True, these species belong to the same order (Falconiformes), which is suggestive that the correlation of forms is determined by their fairly close affiliation and hence a similar response to a single complex of the environmental conditions.

There is one more point that deserves mention. The dark morphs of Falco rusticolus and Accipiter gentilis of polymorphous populations of the northeast Asia are represented by lighter birds compared with other portions of the ranges. Finally, some polytypic species with vast ranges within the boreal zone of Eurasia which are not characterized by coloration morphism are represented in the northeastern Asia by the lightest-coloured strains (Aegolius funereus magnus, Dendrocopos leucotos woznesenskii, Dendrocopos minor immaculatus, Picoides tridactylus albidior, Parus montanus anadyrensis, Parus montanus Kamtschatkensis, Sitta europaea arctica, Sitta europaea albifrons). The above subspecies are characterized by a lighter coloration of the dark parts of plumage and in the case of the normal proportion of white plumage by its hypertrophy. Thus, a clear-out parallelism in the morpho-physiological responses of birds in different systematic groups to an entire complex of the environmental conditions is in evidence. It is most pronounced in species which are characterized by morphism. The extreme northeastern Asia is an area where similar processes of depigmentation in groups of distant affiliation are operating.

In the light of the above well known evidence, it would be interesting to look for other regions where one could observe the development of the processes concerned. But the ranges of numerous species characterized by coloration morphism do not coincide spatially, and hence one can assume from the very outset that there are few sites with a phenotypical effect similar to that observed in the birds in the northeastern Asia.

It makes the prospect of their finding all the more interesting.

Another region with parallelism in the manifestation of avian morphism can be indicated. In the general form, this region can be reffered to as the northern edge of Central Asia. Mountain systems situated in the geographical centre of the Asian Mainland are implied. These are Dzungarian Alatau, Altai, Sayany, Mongolian Altai, Khangai, Khentei. The region concerned is the home of the populations of some widely-distributed species which are characterized by morphism. Interestingly, morphism is recorded either in the populations of this region only, or is manifested there to the greatest extent. The

above is true of Buteo buteo, Falco cherrug, Cinclus cinclus, Turdus atrogularis.

While the correlation of morphism incidence in different species in the northeastern Asia previously received some attention, for the Central-Asian region there are no data available. The situation with respect to each species concerned has been described in systematic surveys, but the parallelism in terms of spatial correlations of morphism have not been emphasized. The latter is worth while doing since the Central-Asian region is the only area in addition to the northeastern Asia where the above effects is observed.

All the four species are represented there by polymorphous populations. In addition to the "normally" coloured species the latter include dark melanistic morphs. Since the problem of the Central-Asian Region has never been considered from this angle before, it is necessary to dwell in more detail on the manifestation of morphism in the above species.

Buteo buteo ranges Eurasia from the Atlantic eastward through Pacific coast northward up to the $62^{nd}$ - $66^{th}$ paralleles, exclusive of Kamchatka, southward to the Mediterranean, Asia Minor, northwestern Iran, in northern Kazakhstan to the $50^{th}$ parallel. Eastward the range covers Tarbagatai, Saur, Dzungarian Alatau, Tien Shan. To the east, the southern boundary passes along the frontier regions of Khangai, Khentei, the middle parts of the Great Khingan, the middle parts of the northeastern China. An isolated portion of the range covers the provinces Gansu, Szechwan, Tzinkhai and eastern Himalayans. It nests in the majority of palearctic islands.

The species is characterized by a complex geographical and individual variability. The phenotypical picture is complicated by the presence of zones of secondary intergradation. In addition, the species is distinguished by morphism, which manifests itself in the presence of three coloration morphs, brown with a rusty tinge and a motley dorsal side; brown, with a tinge of ochre on the ventral side; melanistic, monotonously dark-brown (fuscoater). There are birds of intermediate coloration types, and hence, the discreteness in the manifestation of morphism is not distinctly pronounced here. However it is so marked, that the majority of the individuals display a fairly complete set of diagnostic features of a particular morph.

The melanistic morph is the rarest and its distribution within the species range varies geographically. In places it does not occur at all (northwest of the range). But it is recorded in the majority of the Asian portion of the range although its proportion within polymorphous populations notably varies geographically. In fact in the temperate zone of the European USSR it is 4%, in the Volga Region, and Cis-Urals Territory 13% (Dementiev, 1951). In the Altai and adjacent regions, its contribution to populations notably increases to become maximum within the species range. Based on some data available (Sushkin, 1938) expressed in per cent, the proportion of the melanistic morph in Altai populations roughly is 27-28%. This is the highest percentage within a species range. The above is supported by some older studies (Kaschenko, 1899). Also, a relatively high percentage of this morph is recorded for the Western Sayan area (Sushkin, 1914).

Falco cherrug populates the space of eastern Czechoslovakia, Austria and northern Hungary to the east up to the Great Khingan and to the horth to

Karpathians, Chernigov and southern parts of the Moscow Regions, lower Kama, to the east up to the $52^{nd}$ – $57^{th}$ parallels and to the south to the northern parts of the Balkan Peninsula, northern coast of the Black Sea, Crimea, lower reaches of Don and Volga, east of the Caspian Sea to the south to the Khorosan mountains, northern Afghanistan, Himalayans, eastern Tzinkhai, eastern Gansu.

The species is characterized by pronounced geographical variability, with considerable individual variations. No stable manifestations of morphism are recorded in the populations of the bulk of the range. But in northeastern portions of the species' distribution range, morphism is highly pronounced. There are two colour morphs there: light (common in terms of coloration)and dark melanistic ("altaicus").

As in the previous case, no rigid discreteness in morphism manifestations is recorded there. On the one hand, there are birds which to some extent combine the features of both morphs, on the other, each morph represents a wide range of individual variability, which results alternatively in greater or lesser manifestation of the specific features of the respective type of coloration. But on the whole, the light and dark morphs are to a great extent discrete and the general phenotypic pattern is in conformity with our concepts on the balanced genetic polymorphism of a discrete type. The above is well illustrated by the history of discovery and attempts of taxonomic interpretation of the dark morph status.

This morph was assigned to an independent species (Hierofalco altaicus), and currently it has been regarded either as such or as a geographical strain Falco rusticolus. This discussion of this problem is beyond the scope of the present paper, I shall only point out that the abundant new evidence available leaves no doubt that altaicus is only a morph of the polymorphous populations of Falco cherrug characterized by hypertrophy of melanin coloration compared with other variants of this species.

Polymorphous populations of Falco cherrug populate the area covering Altai, Western and Eastern Sayany, Khangai, Khentei, Tarbagatai, Mongolian and Gobi Altai, Dzungarian Alatau and presumably northern and central Tien Shan. The dark morph is, within the area concerned, accounts for a large proportion of the population, but the actual ratio of the above morph to the light morph has not yet been clarified. There are grounds to believe that its proportion in the localities of the largest numbers of dark-coloured birds (Attai, Khentei, Khangai and Mongolian Altai) attains 20-25% of the population. In that, the northern edge of Central Asia differs from all the other portions of the species' range. Actually, pronounced morphism is characteristic of Falco cherrug only within the region concerned and the melanistic morph displays a rigid geographical localization, being confined to this region alone.

Cinclus cinclus shows a very complicated discrete distribution pattern within Palearctic and northern Indo-Malayan Regions. In northwestern Africa it populates the Atlas Mountains. In Europe, it ranges from the coast of Norway and Northern Seas, the coast of the Bay of Biscay to the Pirenean Peninsula and eastward to the Ural Ridge. To the south this portion of the

range extends to the Mediterranean, southern Carpathians, Baltic Republics, the valley of the Onega River, the upper reaches of Mezen and Pechora (along the Ural Mountains southward to the middle parts of the Southern Urals).The Asia Anterior portion of the range extends from Asia Minor to the Khorosan Mountains and farther northward to the northern piedmont of the Great Caucasian Ridge, the north-facing slope of the Khorosan Mountains, to the south to the southern edge of the Armenian Upland, Zagross Mountains and southern edges of the Khorosan Mountains. The largest section of the range stretches from the western piedmont of Tien Shan, Alai System, Paropamiz and Middle Afghan Mountains eastward to the Aldan-Uchur Ridge, Arguni, Khentei, the ridges Alashan and Tzinlin, the Sino-Tibet mountains, to the north to the ridges: Kirghiz, Trans-Ili, Dzungarian, Tarbagatai, Saura, Northern Altai, Salair, Kuznetsk Alatau, eastward to the north to the $56^{th}$ - $58^{th}$ parallels, southward to the Middle Afgan Mountains, the southern slope of Himalayans, and the Yunan Uplands. It is absent in the vast spaces of deserts within the Middle Asian - Central Asian portion of the range concerned.

The vast range and discrete distribution determine the vast geographical variability of the species. Also, all the populations are characterized by a considerable individual variability range. Morphism is characteristic of the populations of the northeastern portion of the range and is not found in other sites. The polymorphous population inhabits the area from the Salair Ridge, Western Altai and Saur and southeastward to the Aldan-Uchur Ridge, the valley of Arguni, Khentai and northward to the Kuznetsk Alatau, in the Enisei basin to the $56^{th}$ parallel and eastward to the north roughly to the $58^{th}$ parallel; southward to Saur, Mongolian Altai, Khangai, Khentei. Within the area concerned, morphism manifests itself to a variable extent, fluctuation geographically.

But before discussing this problem a brief description of the types of coloration should be given. There are six of them (Stepanyan, 1977): 1) The lower side of the body (throat, lower side of neck, chest, belly) is white. 2) The lower side of body (throat, lower side of neck, chest, belly) is white, with a brownish tinge on the belly. 3) The throat, lower neck and chest are white, belly light brown, the boundary between the zones of white and brown coloration not being very distinct. 4) The throat, lower neck and chest are white (occasionally chest is darkened by brownish specks or a touch of brown); the belly is brown, the boundary between the zones of white and brown coloration sharp; 5) The throat, lower side of neck and chest are light-brown, belly dark-brown, the boundary between these two zones being sharp enough. 6) The throat, lower side of neck, chest and belly are brown, coloration of the throat, lower neck and chest, only somewhat lighter than the stomach, the boundary between these two coloration zones not being pronounced (the morph represents the most melanistic coloration type).

As can be seen from the above descriptions, the phenotypic pattern of the polymorphous population ie exceptionally complex. The birds of all the coloration types occur within a single region (one should bear in mind that the population is largely sedentary). That has led to a good deal of taxonomic and nomenclature confusion, since practically for all the types of coloration, nomenclature units for geographical strains or even species were

1246

proposed (biedermanni, bilkevitchi, middendorfii, bianchii, baicalensis, ki-borti, saturatus, leucogaster). The taxonomical aspect of the problem is not considered here, but dealt with in a special paper (Stepanyan, 1977).

There is no distinct alternation in the manifestation of the described types of coloration. Generally speaking, the discreteness of morphism in this case is less distinct than in the two previous cases. Nevertheless, in the local populations, birds of all the coloration patterns are invariably found, suggesting that the situation concerned can be described as a balanced genetic polymorphism.

As noted above, the spatial dispersal of morphs within the northeastern portion of the range varies geographically. The maximum diversity of coloration types and concurrent maximum relative and absolute numbers of the darkest melanistic morph (coloration type 6) is recorded in Saur, Altai, Mongolian Altai, Khangai and Khentei. Here, birds with purely white lower side of the body (coloration type 1) are rare, while melanistic individuals (coloration types 2-6) prevail. Notably, both westward (Central Asia) and eastward (Trans-Baikal Territory)and farther to the east of this region,the variability of populations sharply declines, and in both cases, there white-bellied individuals of coloration type 1 are either dominants or are exclusively represented (Central Asia).

The above complex geographically-phenotypical pattern clearly displays the association of the darkest melanistic morph with the above geographical centre of the Asian Mainland. As has been mentioned above, both absolute and relative incidence of this morph are highest in this region. On the whole, the range of melanistic morph, has almost not extended beyond the mountain regions of Saur, Altai, Mongolian Altai, Khangai and Khentei. Turdus atro-gularis ranges from the upper reaches of Kama and western piedmont of the Ural Ridge eastward to the upper reaches of the lower Tunguska and Baikal, northward to the $62^{nd}$ to $67^{th}$ parallels, southward in the Ural Ridge to the $59^{th}$ parallel to the regions of Tyumen and Barnaul, Tarbagatai, Saura, southern and southeastern edges of Altai and the ridge of Tannu-Ola.

Despite the rather vast range, the species is not characterized by considerable geographical variability. Irrespective of the fact whether this form is assigned to an independent species or a geographical strain of the complex Turdus ruficollis (as is done by some authors), no taxonomic populations can be distinguished within it. Here, Turdus atrogularis is accepted as a monotypic species. Except for some age and seasonal variation of coloration, the individual variability is not distinctly pronounced in the species in question.

That makes the discovery of morphism in this species all the more interesting. In addition to birds with a common coloration type, there occur individuals in which the entire head, the posterior neck, anterior back, throat and upper chest are coloured black as a single colour field. The degree of manifestation of this type of coloration ("relicta") varies with regard to the general space occupied by the black colour. But in all these cases, the birds thus coloured differ considerably from individuals with common (most widely dispersed coloration). The numbers of such melanistic

individuals are low, they constituting only a small percentage of polymorphic populations.

The absolute numbers and percentage of the melanistic morph are the highest in the region of Altai and Sayany (Portenko, 1981). Actually, the population of this region alone can be considered truly polymorphous.

The above data are indicative of spatial coincidence of morphism manifestation in the above-considered species. It is noteworthy, that in all cases, a dark melanistic morph is recorded within a polymorphous population. The fact that the polymorphous species considered belong to two different orders (Falconiformes, Passeriformes) does not change the general pattern. Compared with the situation in the northeastern Asia, one can speak more definitely here of the reaction of polymorphous species to the local complex of conditions. The lack of close affiliation among the species considered and a similar pattern of the manifestation of morphism are indicative that a factor of great impact is operating. True, in this case, the local populations of polytypic species which do not show coloration morphism do not provide a complementary pattern as was observed in the extreme northeastern Asia. Nevertheless, the fact of spatial co-existence of melanistic forms in the four above-considered species is a phenomenon which is undoubtedly worthy of attention.

The region concerned is the geographical centre of Asian Mainland. Thus, while the extreme northeast of Asia is an area of correlated manifestation of morphism and the region where the white morphs are localized, the centre of Asia is the region of correlated morphism where melanistic morphs are found. Naturally, the problem of the factors determining the above phenomena and of the adaptive significance is of great interest. No definite inferences in this respect can be made so far.

To conclude, another problem should be touched upon. As was mentioned above, the ranges of species characterized by coloration morphism do not always coincide spatially. But one should not think that if they do coincide, the above correlation is bound to develop toward the above correlations. Different situations may arise. In Primorye, for example, the ranges of Accipiter gentilis and Terpsiphone paradisi overlap. Both these species are characterized by morphism and in both the manifestations of morphism vary geographically. The population of Terpsiphone paradisi in Primorye is dimorphic: in addition to the dark-coloured morph (i.e. common in terms of coloration type) there is also a white morph present here, whose incidence is relatively low. Accipiter gentilis is represented in this region by a non-monomorphic populations with absolutely no incidence of coloration morphism. The local populations of Accipiter gentilis are the darkest within the species. The same applies to Terpsiphone paradisi with respect to the dark morph.

Thus, the conformity of geographical variability of coloration of the Gloger rule only partially applies to the manifestation of morphism. Some specific mechanisms are active here, which are still largely obscure. Morphism in avian plumage is one of the most vivid forms of discrete balanced genetic polymorphism, representing an independent problem.

If morphism of ecological properties readily lends itself to interpretation from the angle of adaptive significance, coloration morphism does not al-
1248

low of any definite interpretation although such attempts are frequently made. In addition, one should not rule out the possibility of the manifestation of morphism as a side product of the polymorphism of physiological properties. And beyond doubt, of particular interest is the genetic aspect of morphism.

SUMMARY

The most conspicuous form of balanced genetic polymorphism in birds is interrupted morphism (see Huxley, 1955) of plumage coloration. It is often characteristic only for a part of population of polymorphic species and is located only in some parts of its range. Cases of spatial sympatry of morphism among polymorphic species with overlapping ranges are of particular interest. Within the limits of nontropical Eurasia one example of the kind is well known, i.e. maximum development of morphism and the highest numbers of white morphism among Accipiter gentilis and Falco rusticolus in the extreme north-east of Asia. Another region where such phenomenon is observed has been also located. It is the northern part of Central Asia (Dzhungarsky Alatau, the Altai, the Sayans, the Khangai, the Khentei). Here the pronounced development of morphism is characteristic for four species, namely: Buteo buteo, Falco cherrug, Cinclus cinclus, Turdus atrogularia. Their local polymorphic populations include melanistic phenotypes which have maximum absolute numbers and rate here. North-east Asia is the area of correlated expression of morphism and the region of localization of white morphs, while northern part of Central Asia (i.e. the geographical centre of the continent) is the area of correlated expression of morphism and the region of localization of melanistic morphs. The regularities of spatial distribution of colour morphs coincide in some cases with general subordination of geographical changes of coloration to Gloger' rule, though in some other cases such coincidence is unpronounced. The adaptive significance of interrupted balanced genetic polymorphism in bird coloration remains vague.

R e f e r e n c e s

Dementiev G.P. Ptitzy Sovetskogo Soyuza. Moscow: Nauka, 1951, 1.
Huxley J. - In: Acta XI Congr. Intern. Ornithol. Basel, 1955, p. 309.
Kaschenko N.F. Results of the Altai zoological expendition of 1899. Vertebrates. Tomsk, Kononov and Skulimsky Publ., 1899.
Portenko L.A. - In: Trudy zoologicheskogo Instituta. Leningrad, 1981, 102, p. 72.
Stepanyan L.S. - Zool. zhurn., 1977, 56, N 12, p. 1834.
Sushkin P.P. Materialy k poznaniyu fauny i flory Rossiyskoi Imperii. Otd. zoologii. Moscow, 1914, vyp. 13.
Sushkin P.P. The birds of Soviet Altai and adjacent parts of northwestern Mongolia, v. 1, Moscow; Leningrad: USSR Acad. Sci. Publ., 1938.

# TYPES OF COLONIALITY IN THE FAMILY LARIDAE

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In 1973-78 the colonial nesting of 18 species of gulls and terms was studied in different regions of the USSR. Coloniality was found to differ in structure and ecology amongst these species of Laridae.

On the basis of both this field data and data in the literature on other species of Laridae it was concluded that two types of coloniality exist in this family. There is obligatory coloniality (OC) and facultative (optional) coloniality (FC). The FC-species can be further divided into dense-nesting and diffuse-nesting species (Fig. 1).

LARIDAE
(Larinae + Sterninae)
87 species

OC-SPECIES
about 16 species
(min. 7 sp.)

L.ichthyaetus
L. relictus
L.genei
? L.(belcheri) atlanticus
R.tridactyla
R.brevirostris
S.sandvicensis
S.maxima
? S.bergii
? S.bengalensis
? S.eurygnatha
? S.elegans
? S.zimmermanni
? A.stolidus
? A.minutus
? A.tenuirostris

FC-SPECIES:

DIFFUSE-NESTING SPECIES
(about 65 species)

DENSE-NESTING SPECIES
about 6 species
(min. 3 sp.)
? L.heermanni
? L.delawarensis
L.brunnicephalus
L.melanocephalus
H.caspia
? S.fuscata

F i g. 1.Species of Laridae with different types of coloniality

The characteristic features of OC-species:
- very high nest density (nests often contact one another);
- lack of nesting in solitary pairs;
- nesting only in places where terrestrial predators are absent;
- lack of defended nest territory;
- defecation by the incubating bird on the edge of its nest;
- absence of egg shell removal;
- decrease of the cryptical properties of egg colour and, sometimes, chick colour;
- the existence of special nestling "creches" and "herds" at the appearance of a predator (in species that nest on flat islands);
- absence of cannibalism in most species (as a rule);
- the existence of ichthyophagia or trophic bonds with aquatic systems.

The characteristic features of diffuse-nesting FC-species:
- variety of nest density; nesting in solitary pairs is not unusual;
- nesting in places accessible to terrestrial predators;
- defended nest territory in all species;
- camouflaged nests (defecation on the nest does not occur, egg shells are removed);
- cryptic egg and chick colour;
- chick scattering and hiding with the appearance of predator;
- euryphagia and cannibalism in most species.
The characteristic features of dense-nesting FC-species:
- nest density is greater than in the diffuse-nesting FC-species but less than in OC-species;
- the occurrence of nesting in solitary pairs in some species;
- nesting in places where terrestrial predators are absent;
- defended nest territory in all species;
- absence of defecation on the nest;
- egg shell removal by most species;
- cryptic coloration of eggs and chicks evident but not so pronounced as in the diffuse-nesting FC-species;
- the existence of special chicks "creches" and "herds" in some species;
- cannibalism in some species.
The reason for the variety in colonial structure lies in the different strategies of offspring defence. Larids use two strategies:
A. Protection of eggs and chicks using the "effect of density", i.e. the compact packing of birds frightens away avian predators (ED-strategy), ED-strategy lead to a very high nest density.In this case camouflage of nests and chicks is not necessary. The OC and partly dense-nesting FC are the result of this strategy.
B. Protection of offspring based on the combination of active attack and diffuse distribution of cryptically coloured eggs and chicks (AD-strategy). Diffuse-nesting facultative coloniality is the result of this strategy.
The ED-strategy is effective only against nonspecialized avian predators, that are mainly dangerous for eggs and chicks. If predators are dangerous for adult birds (as in the case of terrestrial predators or in the case of small colonial species) the AD-strategy becomes more effective.
The evolutionary influence of the first type of avian predator has resulted in compaction of colonies of prey species, whereas the evolutionary influence of terrestrial predators has tended to disperse the nests in a colony. The influence of cannibalism of eggs and chicks is intermediate: it condenses the colony but only to the certain limit (Fig. 2).
The following factors influence the choice of evolutionary strategies of offspring defence (Fig. 3):
- resence or absence of terrestrial predators in the places of nesting;
- body size of the colonial species;
- type of feeding (euriphagia in large-bodied and medium-sized species often lead to the cannibalism).
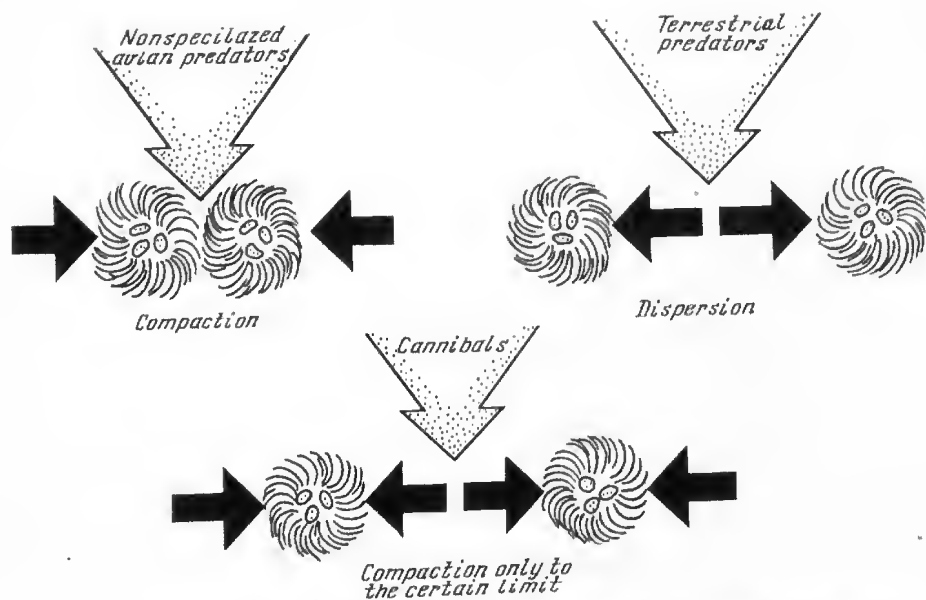
F i g. 2. Influence of predators and cannibals on the nest density
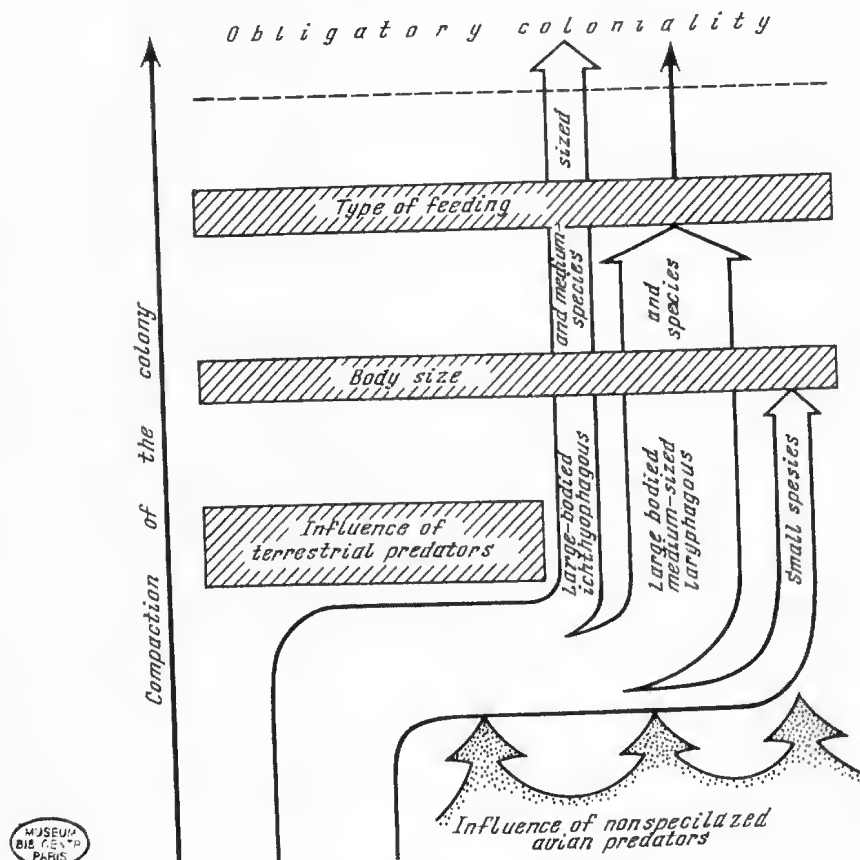


F i g. 3. Influence of the main forming factors on the evolution of coloniality in the family Laridae

ROUND-TABLE DISCUSSIONS


V.M. GAVRILOV

SEASONAL AND CIRCADIAN CHANGES OF THERMOREGULATION IN PASSERINE AND NON-PASSERINE BIRDS; WHICH IS MORE IMPORTANT?

I.H.J. LYSTER, D.T. LEES-SMITH
HOLARCTIC AVIAN SPECIATION ATLAS

G. Th. de ROOS
TOURISM AND BIRDS

S.D. MATVEYEV
SEMISPECIES IN THE AVIAN FAUNA OF THE BALKAN PENINSULA

O.L. SILAJEWA
FOLK AND ONOMATOPOEIC NAMES OF BIRDS

S.M. SMIRENSKY
WORKING GROUP ON CRANES OF THE USSR

E.D. MORENKOV
MORPHOFUNCTIONAL ORGANISATION OF THE VISUAL SYSTEM IN BIRDS

SEASONAL AND CIRCADIAN CHANGES OF THERMOREGULATION
IN PASSERINE AND NON-PASSERINE BIRDS; WHICH IS MORE IMPORTANT?

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Accumulation of laboratory data on energy expenditure by animals under standard conditions have proved valuable in field ecological studies too, particularly in calculating energy budgets in free-living birds. But their correct use requires correct ecological interpretation and evaluation.

In 1970 Ashoff and Pohl(1970) selected from a relatively large body of evidence on basal metabolism in different species of passerine and non-passerine birds, a relatively small number of measurements where basal metabolism was measured in each species under study in standard conditions during the daytime and at night. They obtained differences in the level of basal metabolism as a function of the time of measurement. The nocturnal basal metabolism proved to be 25% lower than diurnal.

S.C.Kendeigh, V.R.Dólnik and I (1977) showed seasonal fluctuations of nocturnal values for basal and standard metabolism, heat conductivity and lower critical temperature in a relatively large number of passerine and non-passerine birds.

In 1981, I showed (Gavrilov, 1981) in 18 passerine and 12 non-passerine species that circadian fluctuations are characteristic not only of basal metabolism, but also of heat conductivity, energy expenditure at rest at 0°C, as well as at upper and lower critical temperatures and that of the body within a single season (winter) (Gavrilov, 1979, 1980, 1982).

The purpose of the present communication is to estimate the circadian fluctuations of thermoregulation in the same species during two seasons (winter and summer).

Analysis is deliberately based on my own data, since it was not my intention to obtain differences in nocturnal vs.diurnal measurements; and other special studies are not uniform in either reporting such differences, if it is the purpose of the investigator to reveal them, or else, in neglecting such differences, if considered immaterial.

MATERIAL AND METHODS

We studied 18 passerine species covering almost the entire order's range and 12 non-passerine ones with a similar size range (33-1,132 g). The sample included almost equal proportions of north-distributed species and those distributed in the south despite the fact that their patterns of distribution in the size series differed. Among the small species, which are mostly non-passerine, there is a greater proportion of southern species, while large-sized birds are mostly northern.

All the bioenergetic indices were obtained by measuring oxygen consumption in birds captured mostly on the Baltic shore or from the Moscow Zoo collection. The birds had been maintained in open aviaries for at least 4 weeks prior to the experiments. Tropical, subtropical and migratory birds were maintained at 10-22°C during winter. In winter (from December to February), only non-moulting birds were used in the experiments, and in summer, measure-
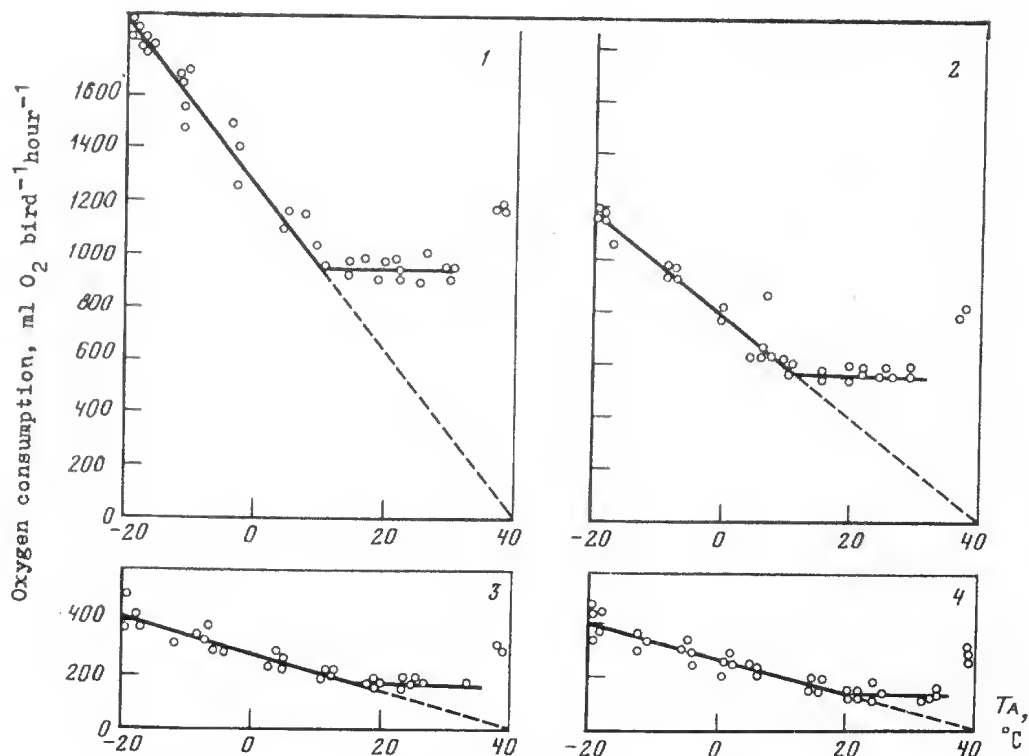
F i g. 1. Oxygen consumption as a function of ambient temperature ($T_A$, °C) of summer acclimatized in <u>Corvus corax</u> (1), <u>Corvus corone cornix</u> (2), <u>Turdus merula</u> (3), <u>Turdus philomelos</u> (4) at night. Dotted lines show the correspondence of Scholander model

ments were made in late June through early July, i.e. between the termination of breeding activity and onset of moult. Oxygen consumption was measured at different phases of the circadian cycle only in starved birds, which completed assimilation of food; in some specially documented cases, birds, which did not complete assimilation, were measured as well. Large birds were made to fast 12 hours and the small ones - 3 to 4 hours prior to their measurements. The birds (one at a time) were placed first in special cages, then in air-tight chambers of acrylic plastic for measuring oxygen consumption in the dark. The chambers varied in size from 3 to 25 $\ell$ depending on the size of birds. The chambers were installed in refrigerators or thermostats, where the needed temperature was pre-set. Before measurements, the air was pumped through the chambers for two hours in order to stabilize the temperature. Oxygen consumption was measured with a modified Kalabukhov instrument (Kalabukhov, 1951); each measurement at the same temperature lasted 1-4 hours, with intervals between measurements from 1.5 to 2 hours. Within a single temperature cycle, oxygen consumption was only registered with 5°C elevations of ambient temperature in a step-like manner. The number of individuals studied per species was 2-4 in some hard-to-get at species, and 8-10 and more in others. The correlation of thermoregulation indices was in agreement with

the Newton model as modified by Scholander et al. (1950) and as shown in Fig. 1. In some cases in large birds, especially in the daytime, measurements deviated from that model. Data on oxygen consumption were transformed into energy terms: 1 cm$^3$ $O_2$ = 20.1 J.

Body temperature was measured with a thermistor introduced into the cloaca and attached to the tail. Registration was long-range, using a direct current bridge.

The relationship between thermoregulation values and body weight was estimated separately for passerine and for non-passerine birds, for winter vs. summer and daytime vs. nighttime measurements. The relationship between thermoregulation values and body weight was estimated according to the method of least squares, assuming that all the dependences are expressed by a power function $M = a \, m^b$, where M is a thermoregulation index, m – body mass, a and b, empirically obtained constants, with a setting the regression level, and b – the slope.

RESULTS AND DISCUSSION

Circadian fluctuations of thermoregulations within a single season (winter).

Let us first consider fluctuations of thermoregulation as shown in Fig.1 within the same season but at different times of the day, under different illumination and depending on the gut content.

In winter a normal diurnal cycle of energy expenditure at rest is a weakly expressed two-peak rhythm with maxima at the beginning and at the end of the day (Fig. 2). Higher metabolism during the daytime persists when the birds are maintained in the dark for more than 24 hours. This is indicative of the fact that changes in the metabolic level are circadian. During the day and without food the level of diurnal metabolism may be only 10-15% higher than that of nocturnal.

The presence of food in the digestive tract changes the level of metabolism (Table 1). Immediately after feeding, metabolism is found to increase. In this case the energy of a specific dynamic action augments oxygen consumption and may promote maintaining heat balance under low temperatures of the ambient medium. In smaller species, the after-feeding energy expenditure following feeding in the thermoneutral zone approaches the basal level more rapidly, presumably due to a lesser capacity of the digestive tract. The species fed with meat or hen eggs prior to the experiments (Corvidae and Turdidae) exhibited higher oxygen consumption than those fed with grain mixtures (Galliformes, Ploceidae, finches and parrots). This reflects a higher degree of energy of the specific dynamic action effect of animal food compared with grain. In insectivorous birds, energy costs approach the basal level quicker than in granivorous ones of the same size, presumably due to the different rate of food passage through the digestive tract in these groups, and also due to the different rate of digesting these foods.

Body temperature shows a similar circadian cycle, changes in body temperature being closely correlated with metabolic changes (Fig. 2). It should be
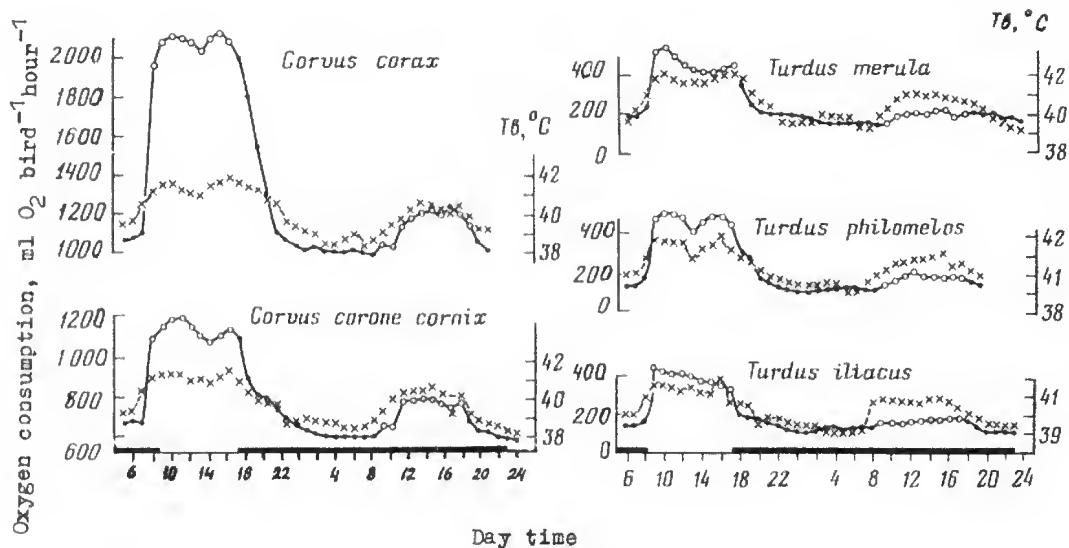
F i g. 2. Changes of oxygen consumption (points) and body temperature (cross) as a function of time in some species in winter. White abscissa – light, black abscissa – dark

T a b l e  1. Changes of resting metabolic rate in darkness after feeding

| Species | Resting metabolic rate in darkness at ambient termperature 22°C, ml $O_2$ hour$^{-1}$ | | | | | |
|---------|--------|--------|--------|--------|--------|--------|
| | at once after feeding | in 2 hours | in 4 hours | in 6 hours, in night | in 12 hours, in night, NBM | in 12 hours, in the day-time, DBM |
| Excalfactoria chinensis | 131.7 | 127.9 | 122.5 | 109.6 | 105.0 | 125.0 |
| Coturnix coturnix | 184.2 | 186.9 | 180.8 | 179.8 | 148.3 | 177.1 |
| Legopus lagopus | 812.5 | 751.7 | 771.0 | 713.3 | 514.8 | 681.5 |
| Melopsittacus undulatus | 111.5 | 109.0 | 85.4 | 65.0 | 59.0 | 65.0 |
| Nymphicus hollandicus | 199.6 | 196.5 | 189.8 | 185.0 | 154.6 | 183.1 |
| Estrilda troglodytes | 65.4 | 32.9 | 31.0 | 30.4 | 27.7 | 30.4 |
| Parus ater | 67.7 | 60.0 | 59.0 | 50.2 | 48.5 | 57.3 |
| Taeniopygia castanotis | 59.2 | 53.3 | 44.8 | 43.8 | 41.7 | 46.9 |
| Erithacus rubecula | 91.2 | 66.3 | 54.2 | 55.4 | 50.4 | 54.6 |
| Fringilla coelebs | 96.9 | 91.0 | 91.7 | 85.0 | 79.0 | 85.8 |
| Turdus iliacus | 225.0 | 198.3 | 158.5 | 131.9 | 128.8 | 151.0 |
| Turdus philomelos | 522.9 | 264.6 | 160.8 | 135.8 | 135.4 | 155.8 |
| Turdus merula | 475.0 | 258.3 | 225.0 | 210.4 | 185.4 | 218.7 |
| Corvus corone cornix | 1170.8 | 941.7 | 850.0 | 837.5 | 685.4 | 802.1 |
| Corvus corax | 2139.6 | 1950.0 | 1339.6 | 1335.4 | 1075.0 | 1281.3 |

noted that the circadian rhythm of body temperature is better retained in the dark compared with the rhythm of metabolism.

"Energy cost at rest - ambient temperature" species regressions were obtained for all the species under study both in the daytime and nighttime measurements (Fig. 3, 4; Table 2). The energy costs at rest at $0^{\circ}$, which are beyond the thermoneutrality zone in all the species studied were higher during the day than at night. Presumably, this is explained by the higher body temperature during the day. The energy expenditure at any ambient temperature beyond the thermoneutrality zone is described by the equation $SMR = h(T_b - T_A)$.

Apparently, if $T_b$ increases, the difference $T_b - T_A$, and, hence, SMR increase. In addition, as shown by measurement results, in most cases heat conductivity increases during the day, which is presumably due to spontaneous optomotoric reaction.

During the day, the feathers are pressed against the body closer, the volume of air contained in the plumage is decreased, and heat conductivity is higher. There is practically no difference associated with plumage properties that would increase or decrease the ratio of the diurnal and nocturnal heat conductivity in species under study. Larger birds show a tendency to a somewhat greater increase during the day time compared with the smaller ones (Table 3). This may be associated with greater thickness of the heat-insulating layer in large birds, and secondly, oxygen consumption measurements may be more disturbing to larger birds.

The lower critical temperature shows different fluctuation patterns in nocturnal and diurnal measurements in passerine vs. non-passerine species (Table 2, 3). In non-passerine birds, the diurnal $T_{\ell c}$ is lower than nocturnal, whereas passerine birds show a reverse tendency except the largest ones. It appears that ideally $T_{ec}$ is to have similar values both during the day and at nighttime, since during the day the values of heat conductivity, body temperature and basal metabolism augment. Although the above indices may increase independently, the joint impact of these parameters is not to change the lower critical temperature position on the temperature scale.

The upper critical temperature is 1-2° lower in the majority of species compared with nighttime, which is due to an increase in basal metabolism (Table 2, 3).

During the day basal metabolism augments in all the species, but in the non-passerines under investigation, this increase is greater (Table 2, 3). Larger passerines augment their metabolism during the day time to a somewhat greater extent than smaller birds. Presumably, this is explained by the measurements being more disturbing to the larger birds. On the whole, the circadian basal metabolism in non-passerine birds is 23% higher than at night, and in passerines - by 12% higher (Table 3). These values are somewhat lower than those obtained by Aschaff and Pohl (1970).

The relationship between thermoregulation indices and body weight (Table 4) demonstrate that in passerines SMR, h, $T_{uc}$, BMR as measured diurnally and nocturnally, fluctuate with a similar regression slope, and it is the regression level that is changing. $T_{uc}$ in them decreases during the day-
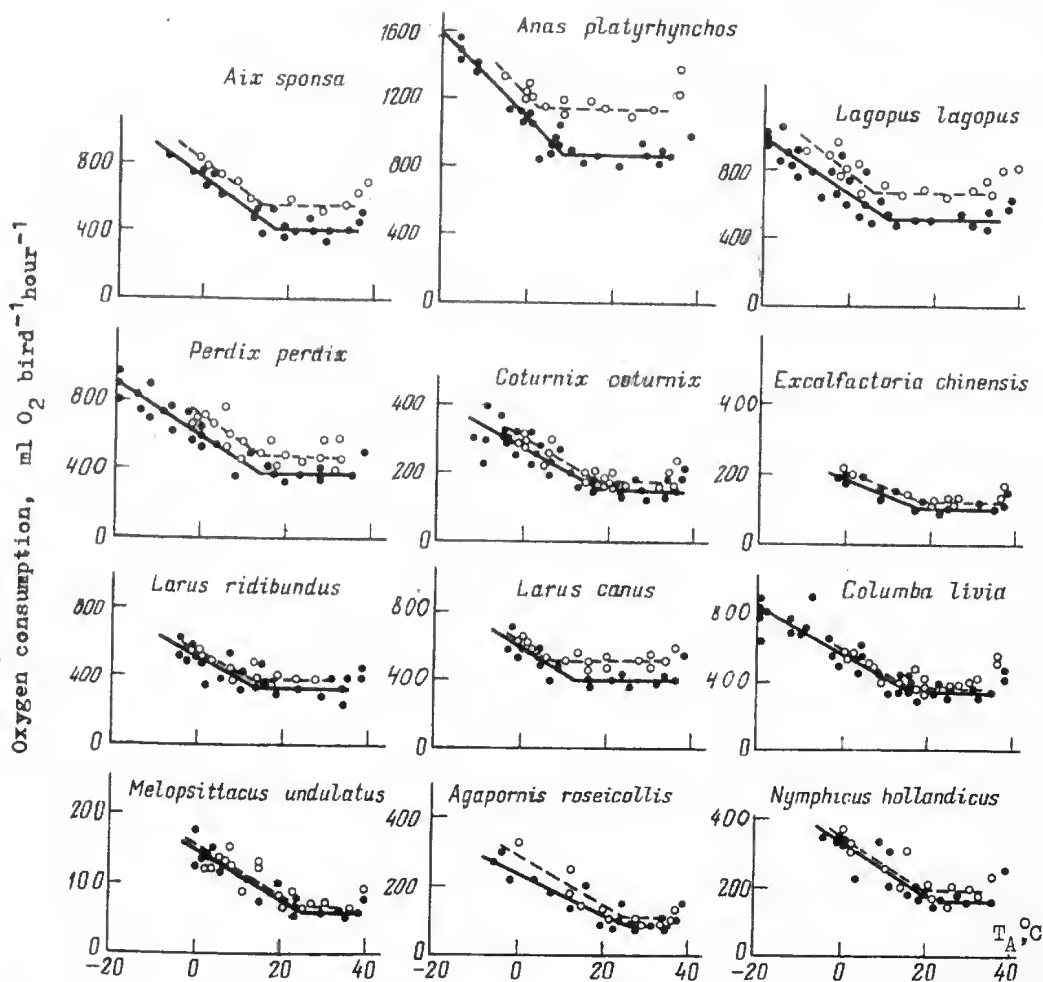
**F i g. 3.** Dependence of energy expenditure at rest on ambient temperatures ($T_A$, °C) in winter in <u>Non-Passeriformes</u>: daytime (white circles), nighttime (black circles)

time with a greater increase in size than at night. In non-passerines, SMR, h and $T_{uc}$ change in a similar way as in passerines, but in nocturnal measurements, BMR increases with an increase in size to a greater extent than in nocturnal. This results in a change in the power index of the respective dependence (Table 4). The diurnal BMR of non-passerines is approximately equal to the nocturnal one of passerines, but it increases with an increase of the bird size to a greater extent.

Analysis of the relationship between and SMR and body weight for diurnal vs. nocturnal measurements in passerines and non-passerines demonstrates that the respective diurnal and nocturnal indices in these avian groups do not differ significantly. The diurnal lower critical temperature in non-passerines (the lowest one) is higher than the diurnal or nocturnal $T_{lc}$ of passerines (bird size being equal). The upper critical temperature in non-passerines is higher than the respective $T_{uc}$ (diurnal or nocturnal) of passerines. Thus, the difference in the level of basal metabolism between these two groups manifests itself not in different energy expenditure under lower
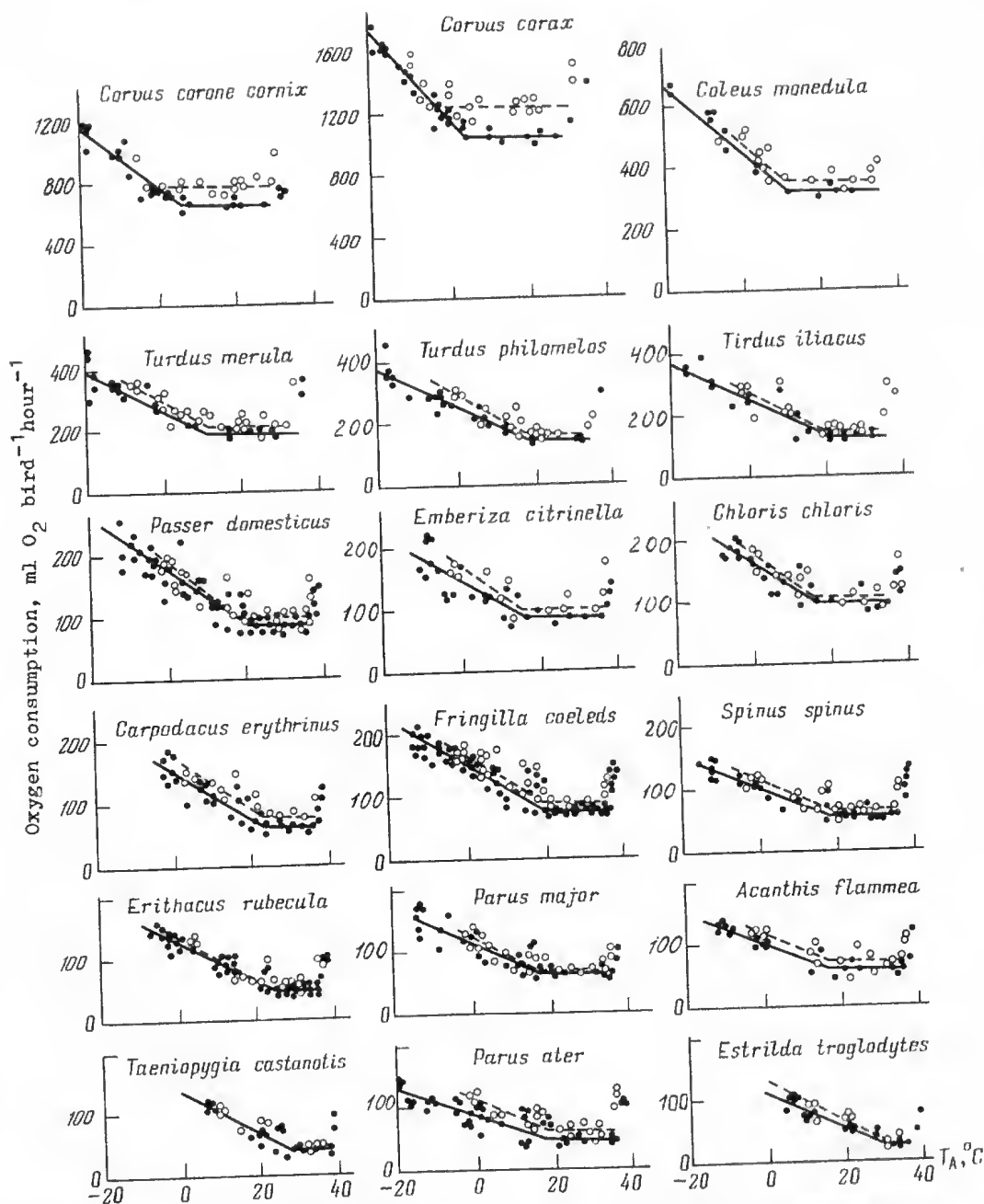
F i g.4. Dependence of energy expenditure at rest on ambient temperatures in winter in <u>Passeriformes</u>:daytime (white circles), nighttime (black circles)

temperature or heat conductivity, but in the upper and lower critical temperatures.

The circadian cycle is characteristic not only of basal metabolism, but also of such thermoregulation indices as heat conductivity, energy expenditure during rest at lower temperatures, and the upper and lower critical temperatures of the environment and of the body.

1260

T a b l e  2. Seasonal and circadian changes of thermoregulatory energetics in birds

| Species | Body mass, m, g | Season | Time of measurements | SM, kJ bird⁻¹ day⁻¹ | $h_l$, kJ bird⁻¹ day⁻¹ °C⁻¹ | $h_u$, kJ bird⁻¹ day⁻¹ °C⁻¹ | Critical temperatures Lower °C $T_{lc}$ | Upper °C $T_{uc}$ | BM, kJ bird⁻¹ day⁻¹ | $T_B$, °C | $T_{uc}-T_{lc}$, °C | SM-BM, kJ bird⁻¹ day⁻¹ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
| **Non-Passeriformes** | | | | | | | | | | | | |
| Aix sponse | 448 | S | N | 352.1 | 8.70 | 32.10 | 18.0 | 36.0 | 194.3 | 39.6 | 18.0 | 157.8 |
| | 448 | S | D | 390.9 | 10.58 | 31.64 | 16.0 | 35.0 | 221.5 | 40.8 | 19.0 | 169.4 |
| | 468 | W | N | 357.1 | 8.42 | 34.26 | 17.0 | 36.0 | 205.6 | 40.2 | 19.0 | 151.5 |
| | 468 | W | D | 402.8 | 10.78 | 34.18 | 12.0 | 34.0 | 273.4 | 40.6 | 22.0 | 129.4 |
| Anas platyrhynchos | 1020 | S | N | 535.9 | 13.16 | 70.34 | 14.0 | 37.0 | 351.7 | 39.8 | 23.0 | 184.2 |
| | 1020 | S | D | 611.0 | 16.28 | 69.27 | 12.0 | 36.0 | 415.6 | 40.1 | 24.0 | 195.4 |
| | 1132 | W | N | 544.3 | 13.61 | 72.67 | 8.0 | 36.0 | 435.4 | 39.6 | 28.0 | 108.9 |
| | 1132 | W | D | 610.9 | 14.65 | 70.86 | 3.0 | 34.0 | 566.9 | 40.3 | 31.0 | 44.0 |
| Excalfactoria chinensis | 44 | S | N | 77.0 | 2.00 | 8.78 | 21.0 | 38.0 | 35.2 | 40.3 | 17.0 | 41.8 |
| | 44 | S | D | 78.6 | 2.39 | 5.09 | 18.0 | 35.0 | 35.6 | 40.5 | 17.0 | 43.0 |
| | 41 | W | N | 94.6 | 2.32 | 12.67 | 19.0 | 38.0 | 50.7 | 39.9 | 19.0 | 43.9 |
| | 41 | W | D | 100.5 | 2.23 | 12.06 | 18.0 | 37.0 | 60.3 | 40.3 | 19.0 | 40.2 |
| Coturnix coturnix | 97 | S | N | 154.1 | 3.85 | 19.26 | 20.0 | 38.0 | 77.0 | 40.1 | 18.0 | 77.1 |
| | 97 | S | D | 151.0 | 3.57 | 13.87 | 10.0 | 36.0 | 83.2 | 40.3 | 26.0 | 67.8 |
| | 109 | W | N | 136.9 | 3.44 | 17.90 | 19.0 | 38.0 | 71.6 | 39.8 | 19.0 | 65.3 |
| | 109 | W | D | 148.6 | 3.51 | 17.08 | 18.0 | 37.0 | 85.4 | 40.4 | 19.0 | 63.2 |
| Perdix perdix | 483 | S | N | 373.9 | 9.26 | 51.81 | 18.0 | 38.0 | 207.3 | 39.6 | 20.0 | 166.6 |
| | 483 | S | D | 411.3 | 11.59 | 25.07 | 16.0 | 36.0 | 225.9 | 40.1 | 20.0 | 185.4 |

Table 2 (continued)

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|---|---|---|---|---|---|---|---|---|----|----|----|----|
| Perdix perdix | 501 | W | W | 198.1 | 7.83 | 37.26 | 15.0 | 37.0 | 186.3 | 38.8 | 22.0 | 111.I |
| | 501 | W | D | 356.7 | 8.09 | 33.61 | 15.0 | 35.0 | 235.3 | 40.4 | 20.0 | 121.4 |
| Lagopus lagopus | 524 | S | N | 410.7 | 10.27 | 67.20 | 14.0 | 38.0 | 268.8 | 39.1 | 24.0 | 141.9 |
| | 524 | S | D | 455.9 | 14.26 | 43.77 | 12.0 | 35.0 | 306.4 | 40.0 | 23.0 | 149.5 |
| | 567 | W | N | 330.3 | 8.21 | 49.66 | 10.0 | 37.0 | 248.3 | 38.9 | 27.0 | 82.0 |
| | 567 | W | D | 392.7 | 10.71 | 46.96 | 6.0 | 35.0 | 328.7 | 40.2 | 29.0 | 64.0 |
| Larus ridibundus | 285 | S | N | 290.2 | 7.30 | 57.78 | 16.0 | 39.0 | 173.3 | 38.8 | 23.0 | 116.9 |
| | 285 | S | D | 301.6 | 7.68 | 38.82 | 14.0 | 37.0 | 194.1 | 39.3 | 23.0 | 107.5 |
| | 306 | W | N | 256.2 | 6.36 | 40.20 | 15.0 | 38.0 | 160.8 | 39.1 | 23.0 | 95.4 |
| | 306 | W | D | 271.3 | 6.02 | 32.17 | 13.0 | 36.0 | 193.0 | 39.8 | 23.0 | 78.3 |
| Larus cenus | 428 | S | N | 345.0 | 9.60 | 50.25 | 15.0 | 38.0 | 201.0 | 38.6 | 23.0 | 144.0 |
| | 428 | S | D | 355.4 | 10.02 | 30.71 | 14.0 | 35.0 | 215.0 | 39.0 | 21.0 | 140.4 |
| | 431 | W | N | 256.2 | 7.86 | 48.58 | 13.0 | 38.0 | 194.3 | 38.8 | 25.0 | 61.9 |
| | 431 | W | D | 316.5 | 7.26 | 41.87 | 9.0 | 36.0 | 251.2 | 40.1 | 27.0 | 65.3 |
| Columba livia | 353 | W | N | 276.8 | 6.85 | 40.10 | 17.0 | (38.0) | 160.4 | 39.9 | 21.0 | 116.4 |
| | 353 | W | D | 291.4 | 7.04 | 29.80 | 16.0 | 36.0 | 178.8 | 41.2 | 20.0 | 112.6 |
| | 368 | S | N | 252.8 | 4.76 | 47.73 | 23.0 | 39.0 | 143.2 | 38.7 | 16.0 | 109.6 |
| | 368 | S | D | 281.4 | 6.35 | 38.60 | 20.0 | 38.0 | 154.4 | 40.3 | 18.0 | 127.0 |
| Melopsittacus undulatus | 25.2 | S | N | 80.0 | 2.00 | 8.65 | 27.0 | 39.0 | 26.0 | 39.1 | 12.0 | 54.0 |
| | 25.2 | S | D | 81.6 | 2.14 | 7.00 | 25.0 | 38.0 | 28.0 | 39.8 | 13.0 | 53.6 |
| | 33.6 | W | N | 76.2 | 1.83 | 8.13 | 26.0 | 38.5 | 28.5 | 39.3 | 12.5 | 47.7 |
| | 33.6 | W | D | 79.5 | 2.00 | 6.98 | 24.0 | 37.5 | 41.4 | 40.1 | 13.5 | 48.1 |
| Agapornis roseicollis | 48.1 | S | N | 114.7 | 2.87 | 13.40 | 26.0 | 39.0 | 40.2 | 39.0 | 13.0 | 74.5 |
| | 48.1 | S | D | 117.0 | 3.04 | 11.00 | 24.0 | 38.0 | 44.0 | 40.1 | 14.0 | 73.0 |
| | 48.4 | W | N | 113.9 | 2.83 | 13.40 | 25.0 | 39.0 | 40.2 | 38.9 | 14.0 | 73.7 |
| | 48.4 | W | D | 150.7 | 4.24 | 10.64 | 26.0 | 37.0 | 53.2 | 39.3 | 11.0 | 97.5 |
| Nymphicus hollandicus | 85.6 | S | N | 149.9 | 3.77 | 19.83 | 24.0 | 39.0 | 59.5 | 39.2 | 15.0 | 90.4 |
| | 85.6 | S | D | 154.4 | 3.71 | 13.08 | 24.0 | 37.0 | 65.4 | 40.3 | 13.0 | 89.0 |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nymphicus hollandicus | 94.3 | W | N | 164.5 | 4.09 | 24.84 | 22.0 | 39.0 | 74.5 | 39.4 | 15.0 | 90.0 |
|  | 94.3 | W | D | 172.9 | 4.23 | 17.66 | 20.0 | 37.0 | 88.3 | 40.3 | 17.0 | 84.6 |
| **Passeriformes** | | | | | | | | | | | | |
| Estrilda troglodytes | 7.5 | S | N | 52.3 | 1.31 | 3.24 | 30.0 | 38.0 | 13.0 | 40.3 | 8.0 | 39.3 |
|  | 7.5 | S | D | 56.7 | 1.52 | 2.80 | 28.0 | 37.0 | 14.0 | 41.2 | 9.0 | 42.7 |
|  | 7.7 | W | N | 54.4 | 1.37 | 3.35 | 30.0 | 38.0 | 13.4 | 39.9 | 8.0 | 41.0 |
|  | 7.7 | W | D | 64.5 | 1.56 | 2.92 | 32.0 | 37.0 | 14.6 | 41.1 | 5.0 | 49.9 |
| Parus ater | 10.8 | S | N | 46.9 | 1.15 | 4.10 | 23.0 | 37.0 | 20.5 | 40.5 | 14.0 | 26.4 |
|  | 10.8 | S | D | 48.4 | 1.22 | 3.80 | 21.0 | 36.0 | 22.8 | 41.8 | 15.0 | 25.6 |
|  | 11.0 | W | N | 44.4 | 1.10 | 4.69 | 19.0 | 37.0 | 23.4 | 40.8 | 18.0 | 21.0 |
|  | 11.0 | W | D | 51.9 | 1.21 | 5.54 | 20.0 | 37.0 | 27.7 | 41.7 | 17.0 | 24.2 |
| Taeniopygia castanotis | 11.7 | S | N | 78.7 | 2.03 | 3.93 | 29.0 | 37.0 | 19.7 | 39.4 | 8.0 | 59.0 |
|  | 11.7 | S | D | 83.4 | 2.30 | 3.55 | 27.0 | 36.0 | 21.3 | 39.6 | 9.0 | 62.1 |
|  | 11.8 | W | N | 66.2 | 1.65 | 4.02 | 28.0 | 37.0 | 20.1 | 39.5 | 9.0 | 46.1 |
|  | 11.8 | W | D | 67.0 | 1.65 | 4.52 | 27.0 | 37.0 | 22.6 | 39.8 | 10.0 | 44.4 |
| Spinus spinus | 14.0 | S | N | 52.8 | 1.31 | 5.02 | 21.0 | 37.0 | 25.1 | 40.1 | 16.0 | 27.7 |
|  | 14.0 | S | D | 56.0 | 1.49 | 4.60 | 19.0 | 36.0 | 27.6 | 41.0 | 17.0 | 28.4 |
|  | 14.2 | W | N | 51.9 | 1.30 | 4.74 | 18.0 | 36.0 | 28.5 | 40.2 | 18.0 | 23.4 |
|  | 14.2 | W | D | 57.4 | 1.36 | 4.49 | 19.0 | 35.0 | 31.4 | 40.8 | 16.0 | 26.0 |
| Acanthis flammea | 14.0 | S | N | 51.9 | 1.29 | 4.94 | 21.0 | 37.0 | 24.7 | 40.1 | 16.0 | 27.2 |
|  | 14.0 | S | D | 56.1 | 1.47 | 3.81 | 20.0 | 35.0 | 26.7 | 41.3 | 15.0 | 29.4 |
|  | 14.3 | W | N | 59.9 | 1.32 | 4.88 | 17.0 | 36.0 | 29.3 | 40.2 | 19.0 | 30.6 |
|  | 14.3 | W | D | 68.9 | 1.44 | 4.73 | 19.0 | 35.0 | 33.1 | 41.6 | 16.0 | 35.8 |
| Parus major | 16.4 | S | N | 62.4 | 1.56 | 4.76 | 22.0 | 36.0 | 28.5 | 39.8 | 14.0 | 33.9 |
|  | 16.4 | S | D | 67.5 | 1.80 | 3.95 | 20.0 | 34.0 | 31.6 | 41.4 | 14.0 | 35.9 |
|  | 17.1 | W | N | 58.6 | 1.46 | 5.37 | 18.0 | 36.0 | 32.2 | 40.1 | 18.0 | 26.4 |
|  | 17.1 | W | D | 69.8 | 1.51 | 5.09 | 18.0 | 35.0 | 35.6 | 41.2 | 17.0 | 34.2 |

Table 2 (continued)

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Erithacus rubecula | 17.6 | S | N | 73.7 | 1.76 | 5.19 | 25.0 | 37.0 | 26.0 | 39.8 | 12.0 | 47.7 |
| | 17.6 | S | D | 78.1 | 2.13 | 4.85 | 23.0 | 36.0 | 29.1 | 40.9 | 13.0 | 49.0 |
| | 17.6 | W | N | 65.3 | 1.64 | 4.86 | 25.0 | 37.0 | 24.3 | 40.1 | 12.0 | 41.0 |
| | 17.6 | W | D | 74.0 | 1.90 | 4.40 | 25.0 | 36.0 | 26.4 | 41.4 | 11.0 | 47.6 |
| Fringilla coelebs | 21.0 | S | N | 73.3 | 1.82 | 5.37 | 22.5 | 36.0 | 32.2 | 39.6 | 13.5 | 41.1 |
| | 21.0 | S | D | 78.5 | 1.98 | 6.50 | 20.0 | 36.0 | 39.0 | 40.1 | 16.0 | 39.5 |
| | 20.8 | W | N | 77.0 | 1.95 | 6.35 | 20.0 | 36.0 | 38.1 | 39.9 | 16.0 | 38.9 |
| | 20.8 | W | D | 87.9 | 2.11 | 5.93 | 22.0 | 35.0 | 41.5 | 41.9 | 13.0 | 46.4 |
| Carpodacus erythrinus | 21.2 | S | N | 85.0 | 2.13 | 7.95 | 25.0 | 38.0 | 31.8 | 39.8 | 13.0 | 53.2 |
| | 21.2 | S | D | 94.2 | 2.50 | 7.32 | 23.0 | 37.0 | 36.6 | 40.8 | 14.0 | 57.6 |
| | 21.6 | W | N | 78.3 | 1.97 | 7.74 | 24.0 | 38.0 | 31.0 | 39.7 | 14.0 | 47.3 |
| | 21.6 | W | D | 81.2 | 2.00 | 5.52 | 24.0 | 36.0 | 33.1 | 41.0 | 12.0 | 48.1 |
| Passer domesticus | 26.5 | S | N | 92.1 | 2.27 | 8.21 | 22.5 | 37.0 | 41.0 | 40.1 | 14.5 | 51.1 |
| | 26.5 | S | D | 96.5 | 2.46 | 7.87 | 20.0 | 36.0 | 47.2 | 40.4 | 16.0 | 49.3 |
| | 26.4 | W | N | 90.4 | 2.29 | 7.05 | 21.0 | 36.0 | 42.3 | 39.6 | 15.0 | 48.1 |
| | 26.4 | W | D | 94.6 | 2.30 | 6.40 | 22.0 | 35.0 | 44.8 | 40.6 | 13.0 | 49.8 |
| Emberiza citrinella | 26.8 | S | N | 77.5 | 1.94 | 7.54 | 20.5 | 37.0 | 37.7 | 39.9 | 11.5 | 39.8 |
| | 26.8 | S | D | 82.6 | 2.07 | 7.22 | 19.0 | 36.0 | 43.3 | 40.2 | 17.0 | 39.3 |
| | 27.4 | W | N | 71.6 | 1.78 | 7.18 | 16.0 | 36.0 | 43.1 | 49.2 | 20.0 | 28.5 |
| | 27.4 | W | D | 87.5 | 2.24 | 7.06 | 17.0 | 35.0 | 49.4 | 41.0 | 18.0 | 38.1 |
| Chloris chloris | 28.2 | S | N | 81.2 | 2.03 | 6.84 | 20.0 | 36.0 | 41.0 | 39.6 | 16.0 | 40.2 |
| | 28.2 | S | D | 88.6 | 2.62 | 6.63 | 16.0 | 35.0 | 46.4 | 40.3 | 19.0 | 42.2 |
| | 29.0 | W | N | 80.4 | 2.15 | 8.03 | 16.0 | 36.0 | 48.1 | 40.0 | 20.0 | 32.3 |
| | 29.0 | W | D | 86.9 | 2.21 | 7.41 | 17.0 | 35.0 | 51.9 | 41.1 | 18.0 | 35.0 |

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|---|---|---|---|---|---|---|---|---|----|----|----|----|
| Turdus iliacus | 54.0 | S | M | 140.2 | 3.69 | 11.86 | 22.0 | 37.0 | 59.3 | 38.7 | 15.0 | 81.1 |
|  | 54.0 | S | D | 148.7 | 4.24 | 10.67 | 20.0 | 36.0 | 64.0 | 39.9 | 16.0 | 84.7 |
|  | 58.0 | S | M | 135.6 | 3.16 | 10.40 | 20.0 | 36.0 | 62.4 | 40.1 | 16.0 | 73.2 |
|  | 58.0 | S | D | 140.7 | 3.40 | 10.40 | 20.0 | 35.0 | 72.8 | 41.0 | 15.0 | 67.9 |
| Turdus philomelos | 62.8 | S | M | 132.3 | 3.31 | 12.56 | 21.0 | 37.0 | 62.8 | 39.2 | 16.0 | 69.5 |
|  | 62.8 | S | D | 136.5 | 3.45 | 11.83 | 19.0 | 36.0 | 71.0 | 40.4 | 17.0 | 65.5 |
|  | 64.0 | S | D | 125.6 | 3.09 | 10.89 | 19.5 | 36.0 | 65.3 | 39.9 | 16.5 | 60.3 |
|  | 64.0 | S | D | 137.3 | 3.12 | 10.70 | 20.0 | 35.0 | 74.9 | 41.3 | 15.0 | 62.4 |
| Turdus merula | 82.6 | S | M | 139.0 | 3.45 | 13.40 | 17.0 | 36.0 | 80.4 | 39.1 | 19.0 | 58.6 |
|  | 82.6 | S | D | 148.4 | 3.67 | 11.66 | 15.0 | 34.0 | 93.3 | 40.2 | 19.0 | 55.1 |
|  | 83.0 | S | M | 137.8 | 3.44 | 12.80 | 14.0 | 35.0 | 89.6 | 40.2 | 21.0 | 48.2 |
|  | 83.0 | S | D | 147.4 | 3.49 | 15.07 | 12.0 | 35.0 | 105.5 | 40.8 | 23.0 | 41.9 |
| Coleus monedula | 209.0 | S | M | 233.0 | 5.93 | 26.24 | 18.0 | 37.0 | 131.2 | 39.6 | 19.0 | 106.8 |
|  | 209.0 | S | D | 244.6 | 6.00 | 25.20 | 16.0 | 36.0 | 151.2 | 39.8 | 20.0 | 93.4 |
|  | 215.0 | S | M | 222.7 | 5.63 | 26.80 | 11.0 | 36.0 | 160.8 | 40.0 | 25.0 | 61.9 |
|  | 215.0 | S | D | 241.2 | 6.53 | 23.93 | 11.0 | 35.0 | 167.5 | 40.4 | 24.0 | 73.7 |
| Corvus corone cornix | 518.0 | S | M | 394.4 | 9.78 | 47.82 | 11.0 | 36.0 | 286.8 | 39.3 | 25.0 | 107.6 |
|  | 518.0 | S | D | 422.6 | 10.31 | 47.11 | 9.0 | 35.0 | 329.8 | 39.9 | 26.0 | 92.8 |
|  | 540.0 | W | M | 338.1 | 9.55 | 55.13 | 6.0 | 36.0 | 330.8 | 39.7 | 30.0 | 57.3 |
|  | 540.0 | W | D | 422.9 | 9.00 | 55.27 | 4.0 | 35.0 | 386.9 | 40.1 | 31.0 | 36.0 |
| Corvus corax | 1203.0 | S | M | 629.7 | 15.37 | 79.34 | 10.0 | 36.0 | 476.1 | 33.0 | 26.0 | 153.6 |
|  | 1203.0 | S | D | 686.3 | 16.73 | 74.13 | 10.0 | 35.0 | 518.9 | 40.2 | 25.0 | 167.4 |
|  | 1208 | W | M | 574.5 | 14.03 | 86.39 | 4.0 | 36.0 | 518.3 | 36.4 | 32.0 | 56.2 |
|  | 1208 | W | D | 642.3 | 15.41 | 88.29 | 2.0 | 35.0 | 618.0 | 39.8 | 33.0 | 24.3 |

T a b l e  3. Relation between day-time and hight-time measurements of thermoregulatory energetics in birds

| Species | Season | SM | $h_l$ | $h_u$ | $T_{lc}$ | $T_{uc}$ | BM | $T_B$ | $T_{uc}-T_{lc}$ | SM-BM |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |

**Non-Passeriformes**

| Species | Season | SM | $h_l$ | $h_u$ | $T_{lc}$ | $T_{uc}$ | BM | $T_B$ | $T_{uc}-T_{lc}$ | SM-BM |
|---|---|---|---|---|---|---|---|---|---|---|
| Aix sponsa | S | 1.11 | 2.22 | 0.99 | 0.89 | 0.97 | 1.14 | 1.03 | 1.05 | 1.07 |
|  | W | 1.13 | 1.28 | 1.00 | 0.71 | 0.94 | 1.33 | 1.01 | 1.16 | 0.85 |
| Anas plathyrhynchos | S | 1.14 | 1.24 | 0.98 | 0.86 | 0.97 | 1.18 | 1.01 | 1.04 | 1.06 |
|  | W | 1.12 | 1.08 | 0.97 | 0.38 | 0.94 | 1.30 | 1.02 | 1.11 | 0.40 |
| Exalfactoria chinemsis | S | 1.02 | 1.19 | 0.58 | 0.86 | 0.92 | 1.01 | 1.01 | 1.00 | 1.03 |
|  | W | 1.06 | 0.96 | 0.95 | 0.95 | 0.97 | 1.19 | 1.01 | 1.00 | 0.92 |
| Coturnix coturnis | S | 0.98 | 0.93 | 0.72 | 0.50 | 0.95 | 1.08 | 1.01 | 1.44 | 0.88 |
|  | W | 1.09 | 1.02 | 0.95 | 0.95 | 0.97 | 1.19 | 1.01 | 1.00 | 0.97 |
| Perdix perdix | S | 1.10 | 1.25 | 0.48 | 0.89 | 0.95 | 1.09 | 1.01 | 1.00 | 1.11 |
|  | W | 1.20 | 1.03 | 0.90 | 1.00 | 0.95 | 1.26 | 1.04 | 0.91 | 1.09 |
| Lagopus lagopus | S | 1.11 | 1.39 | 0.65 | 0.86 | 0.92 | 1.14 | 1.02 | 0.96 | 1.05 |
|  | W | 1.19 | 1.30 | 0.95 | 0.60 | 0.95 | 1.32 | 1.03 | 1.07 | 0.78 |
| Larus canus | S | 1.03 | 1.04 | 0.61 | 0.93 | 0.92 | 1.07 | 1.01 | 0.91 | 0.98 |
|  | W | 1.07 | 0.92 | 0.86 | 0.69 | 0.95 | 1.29 | 1.03 | 1.08 | 1.05 |
| Larus ridibundus | S | 1.04 | 1.05 | 0.67 | 0.88 | 0.95 | 1.12 | 1.01 | 1.00 | 0.92 |
|  | W | 1.06 | 0.95 | 0.80 | 0.87 | 0.95 | 1.20 | 1.02 | 1.00 | 0.82 |
| Columba livia | S | 1.11 | 1.33 | 0.84 | 0.87 | 0.97 | 1.08 | 1.03 | 1.13 | 1.16 |
|  | W | 1.05 | 1.02 | 0.74 | 0.94 | 0.97 | 1.11 | 1.04 | 0.96 | 0.97 |
| Melopsittacus undulatus | S | 1.02 | 1.07 | 0.81 | 0.93 | 0.97 | 1.08 | 1.02 | 1.08 | 0.99 |
|  | W | 1.04 | 1.09 | 0.86 | 0.92 | 0.97 | 1.10 | 1.02 | 1.08 | 1.01 |
| Agapornis roseicollis | S | 1.03 | 1.06 | 0.32 | 0.92 | 0.97 | 1.09 | 1.03 | 1.08 | 0.98 |
|  | W | 1.32 | 1.50 | 0.79 | 0.92 | 0.95 | 1.32 | 1.03 | 0.79 | 1.33 |
| Nymphicus hollandicus | S | 1.03 | 0.98 | 0.66 | 1.00 | 0.95 | 1.10 | 1.03 | 0.87 | 0.99 |
|  | W | 1.05 | 1.03 | 0.71 | 0.91 | 0.95 | 1.18 | 1.02 | 1.13 | 0.94 |
| Mean | S | 1.06 | 1.15 | 0.73 | 0.87 | 0.95 | 1.10 | 1.02 | 1.05 | 1.02 |
|  | W | 1.11 | 1.10 | 0.87 | 0.82 | 0.95 | 1.18 | 1.02 | 1.02 | 0.93 |

**Passeriformes**

| Species | Season | SM | $h_l$ | $h_u$ | $T_{lc}$ | $T_{uc}$ | BM | $T_B$ | $T_{uc}-T_{lc}$ | SM-BM |
|---|---|---|---|---|---|---|---|---|---|---|
| Estrilda troglodytes | S | 1.08 | 1.16 | 0.86 | 0.93 | 0.97 | 1.08 | 1.02 | 1.13 | 1.09 |
|  | W | 1.18 | 1.14 | 0.87 | 1.07 | 0.97 | 1.09 | 1.03 | 0.63 | 1.22 |
| Parus ater | S | 1.03 | 1.06 | 0.93 | 0.91 | 0.97 | 1.11 | 1.03 | 1.07 | 0.97 |
|  | W | 1.17 | 1.10 | 1.18 | 1.05 | 0.95 | 1.18 | 1.02 | 0.94 | 1.15 |

Table 3 (end)

| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---|---|---|---|---|---|---|---|---|----|----|
| Taeniopygia casta-notis | S | 1.06 | 1.13 | 0.90 | 0.93 | 0.97 | 1.08 | 1.01 | 1.13 | 1.05 |
|  | W | 1.01 | 0.99 | 1.12 | 0.96 | 1.00 | 1.12 | 1.01 | 1.11 | 0.96 |
| Carduelis spinus | S | 1.06 | 1.14 | 0.92 | 0.90 | 1.03 | 1.10 | 1.02 | 1.06 | 1.03 |
|  | W | 1.10 | 1.05 | 0.95 | 1.06 | 0.97 | 1.10 | 1.01 | 0.89 | 1.11 |
| Acanthis flammea | S | 1.08 | 1.14 | 0.77 | 0.95 | 0.95 | 1.08 | 1.03 | 0.94 | 1.08 |
|  | W | 1.15 | 1.09 | 0.97 | 1.12 | 0.97 | 1.13 | 1.03 | 0.84 | 1.17 |
| Parus major | S | 1.08 | 1.15 | 0.83 | 0.91 | 0.94 | 1.11 | 1.04 | 1.00 | 1.06 |
|  | W | 1.07 | 1.03 | 0.95 | 1.00 | 0.97 | 1.10 | 1.03 | 0.94 | 1.30 |
| Erithacus rubecula | S | 1.06 | 1.21 | 0.93 | 0.92 | 0.97 | 1.12 | 1.03 | 1.08 | 1.03 |
|  | W | 1.04 | 1.03 | 0.91 | 1.00 | 0.97 | 1.09 | 1.03 | 0.92 | 1.16 |
| Fringilla coelebs | S | 1.07 | 1.09 | 1.21 | 0.89 | 1.00 | 1.21 | 1.01 | 1.19 | 0.96 |
|  | W | 1.14 | 1.09 | 0.93 | 1.10 | 0.97 | 1.09 | 1.05 | 0.81 | 1.19 |
| Carpodacus erythrinus | S | 1.11 | 1.17 | 0.92 | 0.92 | 0.97 | 1.15 | 1.03 | 1.08 | 1.08 |
|  | W | 1.04 | 1.01 | 0.71 | 1.00 | 0.97 | 1.07 | 1.03 | 0.86 | 1.02 |
| Turdus iliacus | S | 1.06 | 1.15 | 0.90 | 0.91 | 0.97 | 1.08 | 1.03 | 1.07 | 1.04 |
|  | W | 1.12 | 1.07 | 1.00 | 1.00 | 0.97 | 1.17 | 1.02 | 0.94 | 0.93 |
| Passer domesticus | S | 1.05 | 1.08 | 0.96 | 0.89 | 0.97 | 1.15 | 1.01 | 1.10 | 0.96 |
|  | W | 1.05 | 1.00 | 0.91 | 1.05 | 0.97 | 1.06 | 1.02 | 0.87 | 1.04 |
| Emberiza citrinella | S | 1.07 | 1.07 | 0.96 | 0.93 | 0.97 | 1.15 | 1.01 | 1.03 | 0.99 |
|  | W | 1.22 | 1.26 | 0.98 | 1.06 | 0.97 | 1.15 | 1.02 | 0.90 | 1.34 |
| Chloris chloris | S | 1.09 | 1.29 | 0.97 | 0.80 | 0.97 | 1.13 | 1.02 | 1.19 | 1.05 |
|  | W | 1.11 | 1.10 | 0.92 | 1.06 | 0.97 | 1.08 | 1.03 | 0.90 | 1.08 |
| Turdus philomelos | S | 1.03 | 1.04 | 0.94 | 0.90 | 0.97 | 1.13 | 1.03 | 1.06 | 0.94 |
|  | W | 1.09 | 1.01 | 0.98 | 1.03 | 0.97 | 1.15 | 1.04 | 0.91 | 1.03 |
| Turdus merula | S | 1.07 | 1.06 | 0.87 | 0.88 | 0.94 | 1.16 | 1.03 | 1.00 | 0.94 |
|  | W | 1.07 | 1.04 | 1.18 | 0.86 | 1.00 | 1.18 | 1.01 | 1.09 | 0.87 |
| Coleus monedula | S | 1.03 | 1.01 | 0.96 | 0.89 | 0.97 | 1.15 | 1.01 | 1.05 | 0.87 |
|  | W | 1.08 | 1.16 | 0.89 | 1.00 | 0.97 | 1.04 | 1.01 | 0.96 | 1.19 |
| Corvus corone | S | 1.07 | 1.05 | 0.99 | 0.82 | 0.97 | 1.15 | 1.02 | 1.04 | 0.86 |
|  | W | 1.09 | 1.05 | 1.00 | 0.63 | 0.97 | 1.16 | 1.01 | 1.03 | 0.63 |
| Corvus corax | S | 1.09 | 1.09 | 0.93 | 1.00 | 0.97 | 1.09 | 1.03 | 0.96 | 1.09 |
|  | W | 1.12 | 1.10 | 1.02 | 0.50 | 0.97 | 1.19 | 1.01 | 1.03 | 0.43 |
| Mean | S | 1.07 | 1.12 | 0.93 | 0.90 | 0.97 | 1.12 | 1.02 | 1.07 | 1.01 |
|  | W | 1.10 | 1.07 | 0.97 | 0.98 | 0.97 | 1.12 | 1.02 | 0.92 | 1.05 |

Non-Passeriformes+Passeriformes

| Mean | S | 1.07 | 1.13 | 0.85 | 0.89 | 0.96 | 1.11 | 1.02 | 1.06 | 1.01 |
|---|---|---|---|---|---|---|---|---|----|----|
|  | W | 1.10 | 1.08 | 0.93 | 0.92 | 0.96 | 1.14 | 1.02 | 0.96 | 1.00 |

T a b l e  4.  Dependence of bioenergetical parameters of the body mass in relation to circadian and seasonal rhythms

| Bioenergetical parameters | Season | Non-Passeriformes n=12, lim m 25.2–1132 g | | Passeriformes n=18, lim m 7.7–1208 g | |
|---|---|---|---|---|---|
| | | N | D | N | D |
| SM, kJ bird$^{-1}$ day$^{-1}$ | S | $555.4\ m^{0.5534}$ | $(587.5\ m^{0.56})$ | $530.9\ m^{0.4986}$ | $(568.1\ m^{0.50})$ |
| | W | $472.2\ m^{0.5070}$ | $529.3\ m^{0.5118}$ | $506.2\ m^{0.5052}$ | $529.3\ m^{0.4865}$ |
| $h_l$, kJ bird$^{-1}$ day$^{-1}$ °C$^{-1}$ | S | $13.9\ m^{0.5498}$ | $(15.9\ m^{0.55})$ | $12.4\ m^{0.4921}$ | $(13.9\ m^{0.51})$ |
| | W | $11.8\ m^{0.5340}$ | $12.8\ m^{0.5065}$ | $12.2\ m^{0.4965}$ | $13.6\ m^{0.5049}$ |
| $h_u$, kJ bird$^{-1}$ day$^{-1}$ °C$^{-1}$ | S | $71.0\ m^{0.5808}$ | $(51.8\ m^{0.61})$ | $75.6\ m^{0.6214}$ | $(70.3\ m^{0.65})$ |
| | W | $64.4\ m^{0.5706}$ | $(56.0\ m^{0.58})$ | $68.4\ m^{0.6112}$ | $(66.3\ m^{0.61})$ |
| $T_{lc}$, °C | S | $13.9\ m^{-0.1727}$ | $(12.1\ m^{-0.20})$ | $9.4\ m^{-0.2250}$ | $(8.5\ m^{-0.23})$ |
| | W | $9.2\ m^{-0.3329}$ | $6.65\ m^{-0.4159}$ | $5.1\ m^{-0.3505}$ | $3.0\ m^{-0.5060}$ |
| $T_{uc}$, °C | S | $37.1\ m^{0.0024}$ | $(35.2\ m^{0.0025})$ | $36.6\ m^{-0.0031}$ | $(35.5\ m^{-0.002})$ |
| | W | $35.6\ m^{0.0011}$ | $(33.8\ m^{0.0011})$ | $36.1\ m^{0.0040}$ | $(35.0\ m^{0.042})$ |
| $T_{uc}-T_{lc}$, °C | S | $22.2\ m^{0.1696}$ | $(23.3\ m^{0.17})$ | $27.2\ m^{0.2106}$ | $(29.1\ m^{0.22})$ |
| | W | $28.8\ m^{0.3211}$ | $(29.4\ m^{0.33})$ | $31.1\ m^{0.3501}$ | $(28.6\ m^{0.32})$ |
| BM, kJ bird$^{-1}$ day$^{-1}$ | S | $362.6\ m^{0.7059}$ | $(398.9\ m^{0.71})$ | $459.3\ m^{0.7004}$ | $(514.4\ m^{0.71})$ |
| | W | $341.4\ m^{0.7114}$ | $456.1\ m^{0.7226}$ | $506.2\ m^{0.7081}$ | $554.7\ m^{06884}$ |
| SM–BM, kJ bird$^{-1}$ day$^{-1}$ | S | $193.9\ m^{0.3771}$ | $(203.6\ m^{0.38})$ | $117.3\ m^{0.2671}$ | $(118.5\ m^{0.28})$ |
| | W | $108.8\ m^{0.2011}$ | $(111.0\ m^{0.20})$ | $62.1\ m^{0.1460}$ | $(62.2\ m^{0.21})$ |
| $T_B$, °C | S | $39.64\ m^{-0.0044}$ | $(40.4\ m^{-0.0044})$ | $38.67\ m^{-0.0104}$ | $(39.4\ m^{-0.001})$ |
| | W | $39.12\ m^{-0.0106}$ | $(39.9\ m^{-0.010})$ | $39.48\ m^{-0.0031}$ | $(40.3\ m^{-0.002})$ |

SEASONAL CHANGES IN THERMOREGULATION AT NIGHTTIME

Calculated according to the method of least squares, the relationship between bioenergetic values and weight is given in Table 5 separately in passerines and non-passerines for two seasons. Below are considered the properties of passerine vs. non-passerine adaptations to different seasons. The following bioenergetic indices are compared: energy expenditure during rest-standard metabolism, temperature coefficient of metabolic changes with ambient changes by 1° – heat conductivity (separately for lower and higher temperatures) the threshold of thermoneutrality, the limit of thermoneutrality, energy expenditure in the zone of thermoneutrality – basal metabolism, the width of the zone of thermoneutrality, body temperature and energy costs of thermoregulation at 0°.

Energy expenditure during rest at 0°C or standard metabolism SMR (Fig.5). Both passerines and non-passerines expend a similar amount of energy during rest at 0°C (Table 2, Fig. 6). The principle of seasonal fluctuation manifests itself in equal expenditure, hence, Fig. 5 shows the relationship between energy cost and body weight only for passerines, for which there are more data available. In summer, energy expenditure is 10-12% higher than in winter. The relationship between standard metabolism and body weight in non-passerines has a higher power index 0.54-0.55 (Table 5) due to the fact that the terminal part of the size series in non-passerines is formed by larger birds. The amplitude of seasonal fluctuations of standard metabolism is similar in terms of the absolute value both in passerines and non-passerines.

Heat conductivity at low temperatures ($h_\ell$). Heat conductivity at low temperatures is a temperature coefficient of metabolic rate increase with a temperature decrease by 1°C. Measurements are made under ambient temperatures lower than the threshold of thermoneutrality zone. Since energy expenditure during rest at 0°C is, in the size range under investigation, similar to both passerines and non-passerines, and there is no difference in body temperature, mean heat conductivity estimated for these species shows no differences (Table 2, 3). Seasonal fluctuations of heat conductivity at low temperatures are pronounced in non-passerines (Fig. 6). In summer, their heat conductivity is higher throughout the entire size range and differences increase with an increase in bird size only to a small extent. Passerines show insignificant seasonal deviations from the mean level of heat conductivity, and they have a tendency to exhibiting higher heat conductivity in summer (Fig. 7 ). The slopes of the regression lines concerned are similar to those of the relationship of standard metabolism and body weight. Analysis of species regressions used for the calculation of the respective equations reveals that birds inhabiting higher latitudes exhibit a higher seasonal fluctuation of heat conductivity, which particularly holds for large non-passerines (Table 2).

On theoretical grounds, energy costs of rest at a definite ambient temperature beyond the thermoneutrality zone, particularly at 0°C, vary with body weight, proportionately to body weight in the power 1/2 (Kendeigh, Dolnik, Gavrilov, 1977). It is only passerines that rigidly conform to this rule, while in non-passerines, the equation slope is somewhat steeper. The slope is increased at the expense of larger birds' data, and the larger the birds
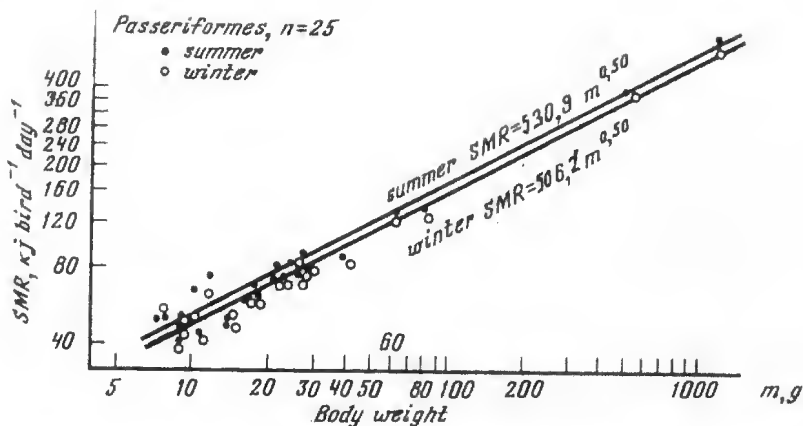
F i g. 5. Regressions SMR on body mass in __Passeriformes__ in summer and in winter
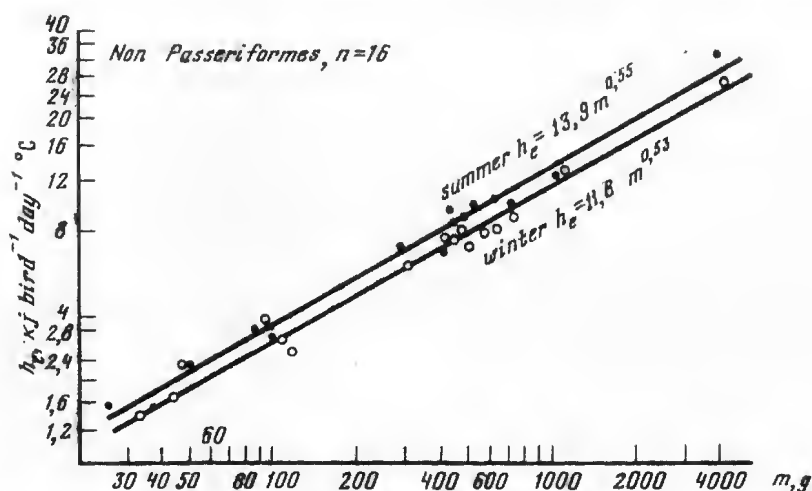


F i g. 6. Regressions $h_1$ on body mass in __Non-Passeriformes__ in summer and in winter
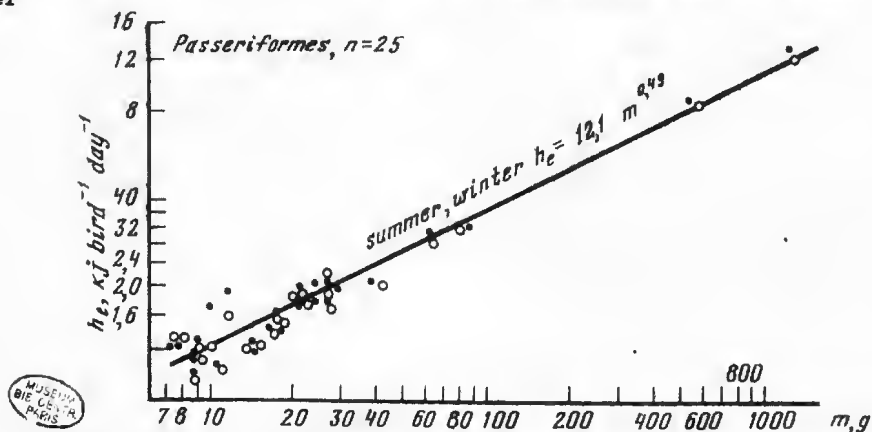


F i g. 7. Regressions $h_1$ on body mass in __Passeriformes__ in summer and in winter

the steeper the curve. Presumably, the change in heat conductivity and energy expenditure during rest at 0°C exhibit two opposite trends related to differences in adaptations of large and small birds to the climate and its seasonal variations. The major adaptations of non-passerine northern species is a drop in heat conductivity in winter; hence, northern birds' data at the extreme portion of the size series render the regression slope steeper.

Heat conductivity at high ambient temperatures ($h_u$). The presence of the zone of thermoneutrality and ability of birds to purposely alter heat irradiation indicate that there is more than one type of heat conductivity. In addition to heat conductivity at lower temperatures, which is minimal, there is another kind of heat conductivity at high temperatures (close to the limit of thermoneutrality zone). Heat conductivity at high ambient temperatures is determined by a deliberate increase in body temperature and evaporative cooling, which is not associated with increased metabolism. Thus, heat conductivity at higher ambient temperatures is heat production at the limit of thermoneutrality zone (which is equal to basal metabolism) divided by the difference between body temperature and that of the environment, i.e. the higher critical temperature: $\frac{BMR}{T_b-T_{uc}}$ . Because the body temperature in the zone of thermoneutrality increases for all the species concerned, the temperature at the upper border of the thermoneutrality zone was assumed to be equal to 42°C. Under such conditions, about half of the heat is dissipated through irradiation, convection and conduction, and the other half – through water evaporation (Gavrilov, 1979).

Heat conductivity at high ambient temperatures is two times as high in small species and 6 to 7 times as high in larger species compared with that at lower temperatures (Table 2). This indicates the greater ability of large birds to alter heat irradiation, and, hence, their possession of a broader zone of thermoneutrality. Seasonal variation of $H_y$ is less pronounced than $H_1$. In Galliformes, heat conductivity at high ambient temperatures is higher in winter than in summer; conversely, in Anseriformes the winter $h_u$ is higher than the summer $h_u$. In other studies of the order concerned, either both situations are recorded, or heat conductivity at high ambient temperatures is not changed seasonally.

No difference between average heat conductivity between passerines and non-passerines is recorded (Table 4). The slope of the equations of the relationship between $h_u$ and body weight is steeper than for $h_1$.

The lower limit of the zone of thermoneutrality($T_{lc}$). There are three relatively idependent factors which determine the position of the limit of thermoneutrality zone: heat conductivity of the integuments, metabolism rate and body temperature. Hence, the lower limit of the zone of thermoneutrality is to be most variable, and this feature can be widely used in adaptations to the body size, climate and season. The principle of seasonal variation is similar both in passerines and non-passerines (Fig. 8, 9). In summer the threshold of the thermoneutrality zone is higher and it varies with variation of body size to a smaller extent. In birds weighing 1 kg, the winter $T_{lc}$ is 4° lower than in summer, both in passerines and non-passerines. Passeriformes have a lower $T_{lc}$, in summer it being similar to that of non-passeriformes in winter. The winter $T_{lc}$ in passerines 1 kg in weight is 4°C
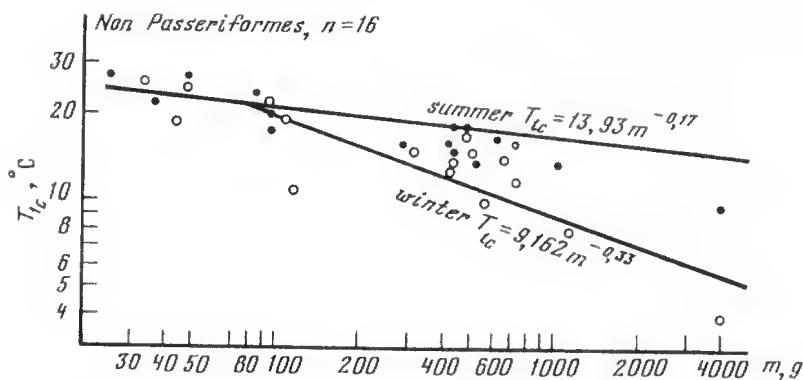
F i g. 8. Regressions $T_{lc}$ on body mass in <u>Non-Passeriformes</u> in summer and in winter
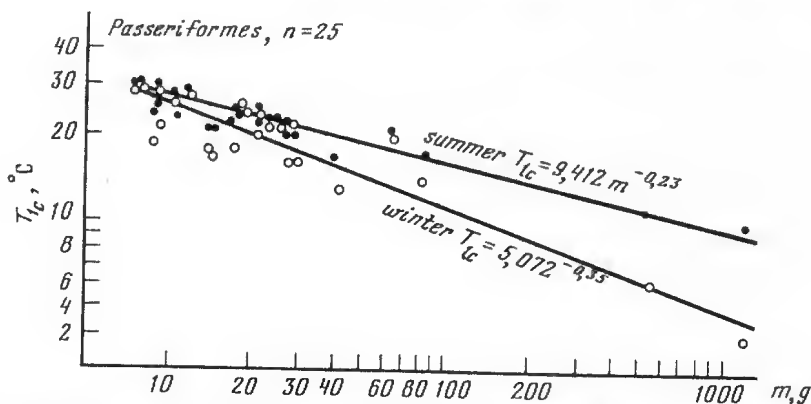


F i g. 9. Regressions $T_{lc}$ on body mass in <u>Passeriformes</u> in summer and in winter

lower than in non-passerines of similar weight. Seasonal fluctuations of $T_{lc}$ are more pronounced and show a more stable trend, compared with fluctuations of heat conductivity and standard metabolism.

<u>The upper limit of the zone of thermoneutrality or the upper critical temperature ($T_{uc}$).</u> The position of the limit of thermoneutrality on the temperature scale is determined by the limit of increase in the heat conductivity of integuments, the limit of adaptive body temperature, the level of water evaporation, which does not involve any special energy expenditure.

We have not found any fluctiation of the threshold of thermoneutrality zone as a function of body weight. Seasonal variations of $T_{uc}$ indicate some small and insignificant tendency to lower $T_{uc}$ in winter compared with summer time. It is also more pronounced in northern birds, both passerine and non-passerine. These variations do not go beyond one degree; hence, there is a reason to believe that $T_{uc}$ does not depend on body size and does not vary seasonally (Table 2, 4).

The <b>lenght</b> of zone of thermoneutrality ($T_{uc} - T_{lc}$). The zone of thermoneutrality is a range of ambient temperatures within which heat production is at an unchanged (basal)level , and changes in heat irradiation with changed ambient temperature are provided by a purposeful elevation of the body
1272
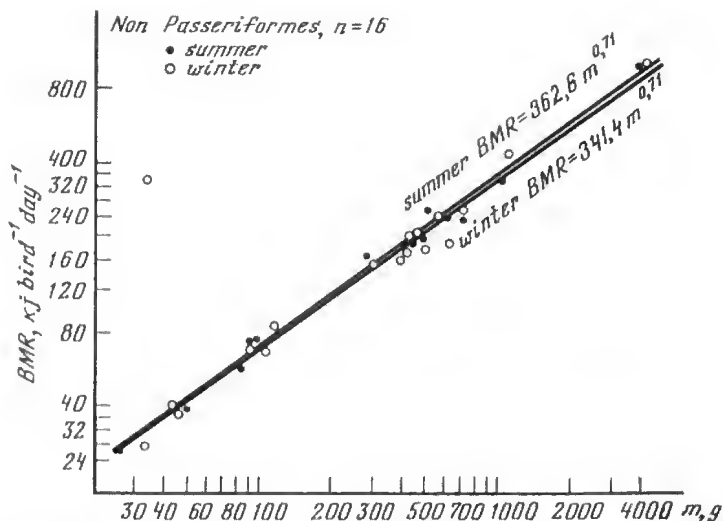
F i g. 10. Regressions BMR on body mass in Non-Passeriformes in summer and winter

temperature and changes in evaporative heat irradiation. The zone of thermoneutrality is a phenomenon characteristic of homoiothermal animals only. The existence of the thermoneutral zone does not follow from the Newton model or from any other model. The length of the zone of thermoneutrality depends on the ability of birds to alter heat irradiation, maintaining the level of heat production unchanged. Because with changes of body size, it is only the thereshold of the zone of thermoneutrality that is shifted, its limit remaining virtually unchanged, the equations for the relationship between the breadth of thermoneutrality zone and body weight will be in principe the reverse of the equations for the relationship between the lower critical temperature and body weight. In winter, both passerines and non-passerines increase their thermoneutrality zone by 4°C, with body weight being equal to 1 kg. In passerines, the zone of thermoneutrality is invariably broader than in non-passerines, suggesting that Passeriformes have a greater possibility of changing the level of heat irradiation without changing heat production. In winter, both passerines and non-passerines retain the level of heat production unchanged at lower ambient temperatures (Fig. 3,4, Table 2). With temperature fluctuating within a wide range, expansion of the zone of thermoneutrality is expedient, particularly in winter.

Basal metabolism (BMR). The Passeriformes and non-passeriformes exhibited different patterns of seasonal BMR rates. On the whole, BMR in passerines is higher in winter and in summer (Table 2, 4 ). Non-passerines (Fig. 10) show partically no seasonal fluctuations of basal metabolism. In summer, BMR is only 6% higher than in winter. Conversely, the winter BMR in passerines (Fig. 11) is 10-12% higher than in the summer one, the power indices in the equations being similar to those of non-passerines. Thus, in summer the basal metabolism of Passeriformes is, on the average, 27% higher than that in non-passerines, while in winter this difference attains 48%. An increase in basal metabolism in winter lowers the threshold of thermoneutra-
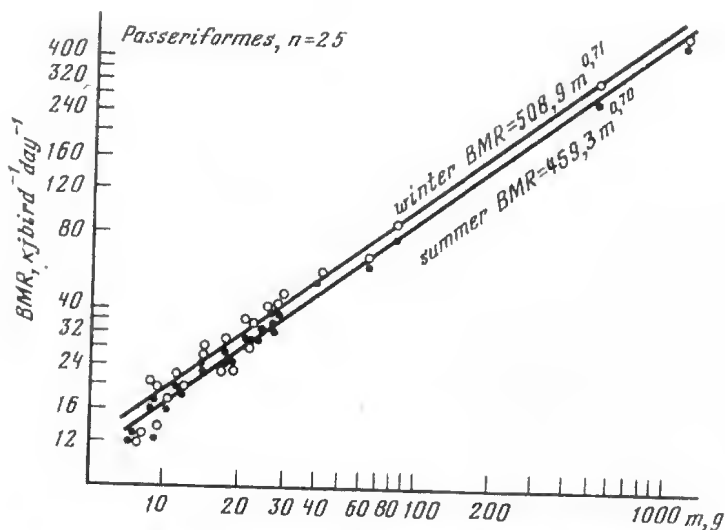
F i g. 11. Regressions BMR on body mass in <u>Passeriformes</u> in summer and in winter

lity zone, expanding this zone. Since heat conductivity of the integuments in passerines and non-passerines is similar, but shows different fluctuation patterns, it is exactly the high basal metabolic rate in Passeriformes that ensures their broader zone of thermoneutrality which covers a broader boundaries of lower temperatures. Thus, an increase in the level of basal metabolism offers an advantage for life under cold conditions, particularly, for small birds, in which heat production - heat irradiation/ratio is unfavourable.

<u>Body temperature</u> ($T_b$). For maintaining the heat balance, birds not only rely on heat production and heat irradiation changes, but also on changes in body temperature. With elecation or lowering the body temperature the birds can respectively develop or not develop hypothermy or hyperthermy,both depending not only on the ambient temperature, but as a function of the season. (see $T_b$ changes in Table 2). Analysis of data on the relationship of body temperature in species under study and body size reveals a very slight tendency to lowering body temperature with an increase in size both in passerines and non-passerines. <u>Passeriformes</u> exhibit an insignificantly lower mean body temperature (Table 2, 4 ). Seasonal variations of $T_b$ are somewhat more pronounced and show a more stable trend in passerines under study in which in winter $T_b$ increases on an average by 0.5 degree. In non-passerines a weak tendency is revealed to lowering body temperature in winter, particularly at low temperatures (in Table 2, the value of $T_b$ is mean body temperature in terms of all the measurements in different body temperature ranges for all the species studied). Seasonal variations of body temperature are presumably not quite adaptive but associated with heat production level, in particular, with the level of basal metabolism.

<u>Energy expenditure on thermoregulation at 0°C (SMR-BMR)</u>. One of the indices of seasonal re-adjustment of metabolism is energy expenditure thermoregulation at a definite ambient temperature, which is beyond the zone of
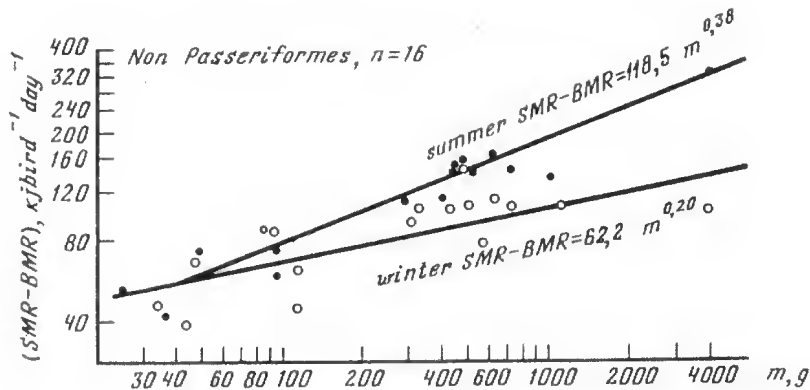
F i g. 12. Regressions SMN-BMR on body mass in <u>Non-Passeriformes</u> in summer and in winter



F i g. 13. Regressions SMR-BMR on body mass in <u>Passeriformes</u> in summer and in winter

thermoneutrality in all the species under study. We have calculated energy costs of thermoregulation at rest at 0°C, which is equal to standard metabolism at 0°C minus basal metabolism. In terms of this index, passerine and non-passerine birds differ only in the level of energy expenditure on thermoregulation, the underlying pattern of seasonal changes being the same (Fig. 12, 13). In summer energy expenditure for thermoregulation is considerably higher than in winter, the difference increasing with an increase in bird size. In Passeriformes, the slopes of regression lines are steep, due to a higher level of basal metabolism, on the one hand, and to the lower threshold of thermoneutrality zone, on the other. The level of energy expenditure on thermoregulation in non-passerines in winter is the same as in passerines in summer. In winter, average energy costs of thermoregulation are 25% lower in passerines compared with non-passerines. This indicates that on the whole the species under study are better adapted to lower ambient temperatures compared with non-passerines.

\*　　　\*　　　\*

Of all the bioenergetic parameters characterizing the metabolism of a resting bird, i.e. standard metabolism, heat conductivity, body temperature, the boundaries of thermoneutrality zone, breadth of thermoneutrality zone, basal metabolism, energy costs of thermoregulation, body temperature is the most stable index, which is not (almost or entirely) dependent on body size and ambient temperature. The fluctuation of all the other indices are aimed at maintaining a stable temperature of the body at different ambient temperatures in different seasons and with different body sizes.

Heat irradiation in standard conditions (i.e. standard metabolism or heat conductivity) of the body devoid of heat-insulation integuments is to increase with an increase in body size, i.e. proportionately to the body size value in the power 2/3. In bodies with heat-insulating integuments, heat irradiation should increase proportionately to the product of body surface by specific heat conductivity of the integuments. Apparently, every species can, adjusting to given ecological conditions, change the specific conductivity of the integuments, breadth of the heat-insulating layer, and hence, change heat conductivity and heat irradiation. Non-passerines gain an advantage by reducing heat-conductivity in winter. In some orders adaptation through seasonal heat conductivity changes are more common, for instance,in Galliformes, presumably due to some features of plumage. Birds with long and mobile feathers are, in addition to seasonal changes of heat conductivity during moult, capable of instantaneous heat conductivity changes through fluffing up the feathers or pressing them against the body. This permits to considerably change the heat conductivity with appreciable fluctuations of ambient temperature. Another adaptation type is changing the heat production level, and not heat irradiation, in response to temperature fluctuations, which is mostly characteristic of the passerines under study.

The optimal zone of ambient temperature is known to be somewhat lower than the threshold of thermoneutral zone. Hence, the threshold of thermoneutral zone exhibits the greatest adaptive seasonal variation. The lowering of the thermoneutral zone threshold in winter is accomplished by non-passerines through reducing heat conductivity of the integuments, and by passerines – through enhancing the basal metabolism rate. With the same mean heat conductivity, passerines, whose basal metabolism rate is 1.3-1.5 times as high as in non-passerines, increase the breadth of thermoneutrality zone by 1.3 to 1.5 times too. Under such conditions, if the thermoneutral zone threshold in a non-passerine bird is equal to 25°C, it will be 19°C in a passerine one. This reduces considerably the optimal range of ambient temperatures, giving an advantage to existence under colder conditions.

Homoiothermal animals are known to maintain adequate energy equilibrium with the environment in every season of the year through two substantially different mechanisms, i.e. seasonal acclimatization and adaptation. Seasonal acclimatization is a seasonal change in the level of adjustment of homeostatic systems developed as a result of natural selection. Acclimatization emerges in response to the impact of environmental cues, or as a result of an endogenous rhythm. Adaptations are a complex of adaptive reactions which originate in response to the impact of primary (selective) factors of the

environment.Adaptations have no seasonal fluctuations and is aimed at maintaining homeostasis at a pre-set acclimatization level.

It can be assumed that seasonal acclimatization in passerines and non-passerines, which manifests itself in lowering the threshold of thermoneutral zone and expanding the thermoneutral zone, is accomplished in passerines via changes of the rate of basal metabolism; and in non-passerines - via changes in heat conductivity. The latter strategy is associated with changes in plumage quality; hence it does not respond so fast to environmental changes in comparison with the basal metabolism rate. A higher level of basal metabolism in passerine birds presumably results in another trend of adaptation to climate seasonality, i.e. the one which falls back upon heat production change, rather than heat irradiation change.


## COMPARISON OF LEVELS IN DAILY CHANGES OF
## THERMOREGULATION INDICES IN DIFFERENT SEASONS

It follows from the above that there are seasonal differences in the level of adjustment of homeostatic systems, which manifest themselves at different thermoregulation indices. On the other hand, each season is characterized by circadian rhythms of metabolism too, which also affect avian thermoregulation. Comparisons of the magnitude of such indices are given in Table 3,4 . Analysis reveals that thermoregulation varies in a wider range seasonally, while its circadian fluctuations are more uniform irrespective of the season. Circadian variation manifests itself in an increase in some parameter or a decrease in others in relation to the level pre-set by seasonal acclimatization. Daily fluctuations are practically similar in passerine and non-passerine species, while the principle of seasonal acclimatization in these two groups may differ.

Hence, it is seasonal fluctuations of thermoregulation that should be primarily taken into account, with subsequent corrections for circadian changes.

R e f e r e n c e s

Aschoff J., Pohl H. - Journ. für Ornithologie, 1970, 111, N 1, S. 38-47.
Gavrilov V.M. - Zool. Zurn., 1979, 58, N 4, 5, p. 530-541, 693-704.
Gavrilov V.M. - In: Ecologia, geographia i okhrana ptitc, 1980, Leningrad,
    p. 73-97.
Gavrilov V.M. - Ornitologia, 1981, N 16. Moscow, p. 42-50.
Gavrilov V.M. - In: Ornithological studies in the USSR, 1982. Moscow,
    "Nauka", p. 377-402.
Kendeigh S.C.,Dolnik V.R.,Gavrilov V.M. - In: Granivorous birds in ecosys-
    tems. Eds. J.Pinowski and S.C.Kendegh. Cambridge University Press,
    p.127-204.
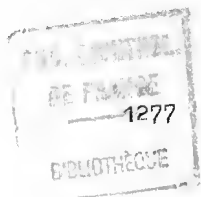
HOLARCTIC AVIAN SPECIATION ATLAS
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The purpose of this atlas is to map, with commentaries, the breeding distributions of the 2014 biological bird species of different biogeographical elements and origins which breed regularly entirely or partly within the Holarctic faunal area (the Palaearctic and Nearctic Regions of classical zoogeographers combined) from the arctic regions south to mid-Sahara, Arabia, Himalayas, west China, south Mexico with the Atlantic Islands and the eoological "islands" of the high montane areas of Taiwan and Chiapas/Guatemala. The atlas is intended as a contribution to better understanding of species evolution and the conservation of environments and gene "pools".

The model for HASA is the two-volumed atlas of speciation in African birds (Hall, Moreau, 1970; Snow (ed.), 1978) published by the British Museum (Natural History). Whilst the various "national", "state" and "provincial" bird atlases of western Europe and North America are pure "gridded" distributional atlases without reference to relationships and evolutions of the taxa dealt with, HASA will not only map species by shading and symbols, but will also comment upon the ecologies and relationships of the species included and consider these in context of current understanding of the climatic and vegetational changes known to have been caused by the advances and retreats of the several Pleistocene glaciations. Morphologically distinct isolated populations are of paramount importance as these could represent stages in the speciation process.

As it is intended that this atlas should incorporate, as far as possible, the most recent data from museum and field studies with these obtained as

efficiently as possible, the preparation work is split between data gathering from museum material, field records and published literature on the one hand and the actual map preparation with commentaries on the other hand. To faciliate data gathering, the entire Holarctic avifaunal area is divided into 306 areas grouped into three categories based upon the extent of ornithological knowledge available for each area. The data so gathered is passed on to specialists in different taxonomic groups who prepare the maps and write the accompanying commentaries.

Whilst the "master" map showing the whole Holarctic avifaunal area (see example attached to report) is based upon the Modified Gall Projection with Equatorial Scale of 1: 110, 000,000, all "subsidiary" maps (outlined upon the example of the "master") will be Equal Area Projection maps with one exception. That exception is the North Polar centered map down to 60N for showing arctic and circumpolar taxa, for which the selected projection is the Zenith Equidistant with scale of 1: 24,000,000 (see map).

Recruitment, on a voluntary basis, of area data collection organizers for areas and of taxonomic group specialists is now in progress; ten years work is envisaged to complete the maps and commentaries ready for publication by
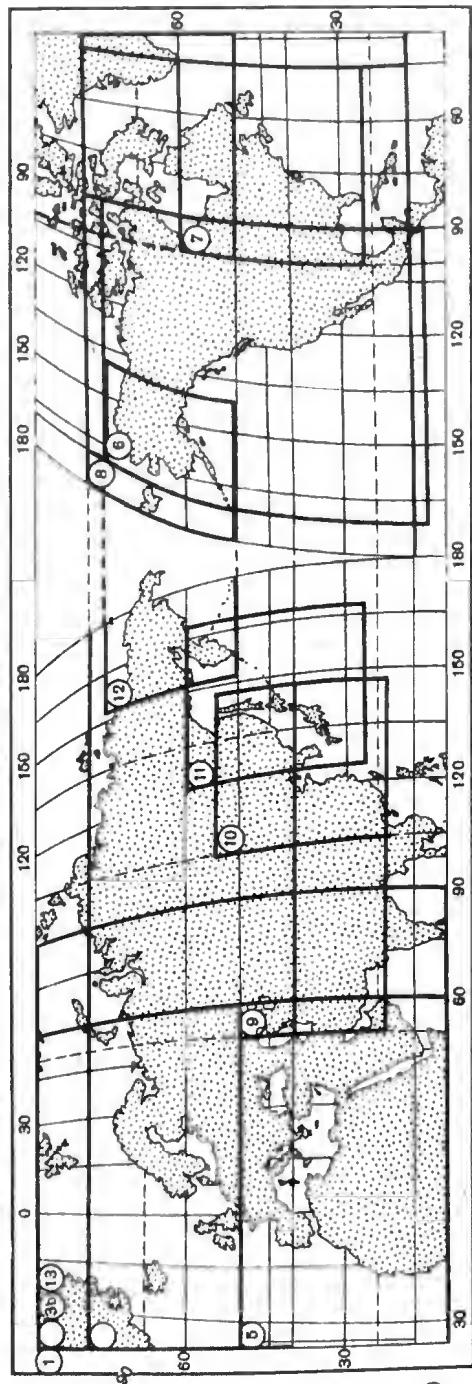
Modified Gall Projection

1 – "Master" map of Holarctic region. 2 – North Polar region, centred down to 60°N (not outlined above).

3a– West Eurasia, North Africa east to 60°E, to include the Urals, Elburz Range, all Arabia and Atlantic Islands.

3b– As 3a, but east to 90°E to certain West Eurasian elements, e.g. Turdus viscivorus. Both 3a and 3b south to 10°N.

4 – North Holarctic excluding "high" arctic; from 75°N south to 40°N, to include tundras and taigas.

5 – South Holarctic; 50°N south to 15°N, to include grasslands, deserts, east-west mountains in Eurasia, western mountains in North America.

6 – West North America eastwards to 90°W; from Alaska and Mackenzie south to Guatemala (10°N).

7 – East North America, from 100°W eastwards, and from 60°N south to include Florida.

8 – All North America from 75°N south to Guatemala.

9 – Central Eurasia from 50°E and 50°N, south to 22°N and east to include S.China and Taiwan (Himalayas, Tibet and the great mountain ranges of Eurasia).

10 – East Eurasia east of 105°E to include Sakhalin, Korea, Japan, Ryu Kya islands; and south of Stenovoi Range to 28°N.

11 – East Eurasian Continental off-shore islands – Kamchatka, Komandors, Kurils, Japanese islands, Ryukyu Retto and the Bonins.

12 – Bering area; 155°E to 140°W and 72°N to 50°N. For N.E.Siberia, Kamchatka, Alaska and the islands of that area.

13 – Eurasia only: to show such transeurasian elements as Dendrocopos major, Aegithalos caudatus species group etc.

1279

an academic or institutional publisher. This ten years' work will be an international effort with ornithologists taking part as ornithologists and not as representatives of institutions or organizations. An advisory committee guides and advises the Organizer/Editor who will work with an executive committee. HASA was formally launched in a round table discussion held on 19 August 1982 in Moscow during the XVIII International Ornithological Congress. HASA is independent of any other institution or organization except the Yorkshire Museum, York, England, which is supporting the expenditure involved in great amount of correspondence and stationary, but offers of funding participants' work will be welcomed and much appreciated.

All offers of participation and funding together with requests for further details sould be addressed to: D.T.Lees-Smith, Organizer/Editor HASA, 134 The Avenue, Starbeck, Harrogate, North Yorkshire HG1 4QE, England.

TOURISM AND BIRDS
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Outdoor-recreation activities increased enormously in the Metherlands as in many other countries, during the seventies. It was decided to study the effects of especially tourism factors upon the presence of breeding wader species like Oystercatcher (Haematopus ostralegus), Curlew (Numenius arquata), Redshank (Tringa totanus) and Kentish Plover (Caradrius alexandrinus) in Holland.

Experimental study plots for the Oystercatcher were carried out and attention was focussed on the following statistical problems: 1) is there sufficient evidence for the statements that higher tourism intensity leads to fewer nests and that positive effects are caused by the no-trespassing signs, 2) if the effects are statistically significant, how should they be estimated by means of confidence intervals. The confidence interval /1.2-4.1/ for the Oystercatcher has been computed, which means that if an area like the experimental duns plots is closed by means of notrespassing signs, then two years later one may expect 1.2-4.1 times as many Oystercatcher nests. The interpretation of e.g. a doubling effect might be that Oystercatchers move to areas where it looks as quiet as possible, e.g. nature reserves.

Other papers dealt with the impact of tourism on seabirds in Galapagos (R.W.Tindle, Charles Darwin Station, Galapagos, Ecuador); direct and indirect consequences of tourist disturbances in gull colonies (J.Latta Hand, University of California, Los Angeles, USA) and with the rate of lessening of birds' fear of men under different conditions (D.V.Vladyshevsky, V.N.Sukachev, Institute of Forest and Wood Siberian Branch of the USSR Academy of Sciences, Academgorodok Krasnoyarsk, USSR).

# SEMISPECIES IN THE AVIAN FAUNA OF THE
## BALKAN PENINSULA

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Semispecies is a genetic term since it was formulated on the basis of genetic data by the Yugoslavian genetisist, Academician Z.Lorković. He also suggested that this term (1958, 1962) should be understood as species not completely isolated, in which genetic interagression is possible. Therefore, in the zone of a sympatric habitat appear not only hybrids, but also the original forms which usually prevail in numbers.

These genetic features distinguish the "semispecies" from the "twin-species" (Stepanyan L.S., 1972) which, according to the author, prove to be reproductively isolated. Nevertheless, Stepanyan admits occasional appearance of hybrids. In my opinion, in such cases the original species are "semi-species" rather than "twin-species".

Some authors erroneously attributed the conjugated term "superspecies" to Lorković. However Lorković believes this term to be superfluous. In a private discussion with Lorković it was found that the "semispecies" should not be understood literally. He holds that "semispecies" are also full-fledged species, but they are of the alopatric origin.

Mayr (1969) also equates the term "semispecies" to the term "allospecies". Since not all allopatric species form interspecific hybrids at the junction of the areas, the author accepts the suggestion of Lorkovic (1962 et in litt.) that the term "semispecies" reflects the status better, i.e. the genetic feature of those species which form hybrids at the junction of the areas.

In the fauna of the Balkan Peninsula I have personally studied hybrids in the following semispecies:

| | |
|---|---|
| Dendrocopus major | – European forests |
| Dendrocopus syriacus | – Mediterranean orchard forests |
| Dendrocopus leucotos | – European forests |
| Dendrocopus lilfordi | – Mediterranean mountainous forests |

(this is a self-contained species, see Matveyev, 1950, 1965, 1967, 1973, 1976).

| | |
|---|---|
| Corvus cornix | – eastern forest steppe |
| Corvus corone | – western forest steppe |
| Passer domesticus | – eastern steppe |
| Passer italiae | – Lombard steppe and apparently |
| Ficedula albicollis | – forests of Central Europe |
| Ficedula semitorquata | – East Mediterranean forests |

Half-collared flycatchers colonize the territory to the west, but their area does not come in contact with that of collared flycatchers and the hybridization is still unknown. Curio (1959) contends that the collared flycatcher is a separate species.

According to the report made by V.M.Loscot (1982) Oenanthe hispanica and Oenanthe pleschanka should be attributed to semispecies.

I personally studied hybrids in the populations at the junction of the areas in the eight indicated species. They lack integradation of features.

Usually, the intensity of their features varies. The number of hybrids is always smaller than that of individuals of the original form. The regression to the initial forms is obvious. The hybridization zone is always narrow. In a pair of "semispecies" the origin is always different, since the speciation occurred geographically remote and ecologicall somewhat different groups of glacial shelters.

For instance, colonization of greater-spotted woodpecker occurred in Holocene starting from Central European refuges and Sirina woodpeckers from eastern refuges. The junction of the areas is located in the northern central part of the Balkan Peninsula and in Asia Minor, but here these species are confined to various altitudinal belts.

CONCLUSIONS

The listed species of birds on the Balkan Peninsula should be attributed to "semispecies". The junction of their areas on the Balkan Peninsula occurred in the Holocene due to their dispersal from geographically remote and ecologically different groups of glacial refuges. "Semispecies" in biological respect are full-fledged species of the allopatric origin. Of the list of twin-species in the European or any other fauna those species should be eliminated which are not quite genetically isolatsd and after studies on the hybrid population at the junction of their areas conform to the term "semispecies" suggested by Lorkovic (1958,1962).

R e f e r e n c e s

Curio E. - Journ. fur Ornith., 1959, 100. Berlin.
Isvestiya na Zoolog. Institut i Muzey BAN. Tom 1-33 (195-1971). Sofia.
Lorkovič Z. Upsala Universitets Arsskift 6, 1958. Upsala.
Lorkovič Z. Wesen, Anwendungbericht und Nomenklatur des Taxons Semispecies.- XI Intern. Kongr. Entom. 1960 in Wien, 1958.
Loskot V. - Abstracts of Symposia. XVIII Congressus Intern. Ornithologicus. Moscow, 1982.
Matvejev S.D. - Academie Serbe des Sciences, Monographies 161. Belgrade, 1950 (en Serbe).
Matvejev S.D. - Novosty ornithologii , AN Kazach. SSR. Alma-Ata, 1965.
Matvejev S.D. - Arkhiv bioloshkich Nauka. Beograd, 1967, 18/2.
Matveyev S.D. - Problems of Evolution, 1972, vol. II, Academy of Sciences of the USSR,Siberian Branch. Novosibirsk. ( in Russian).
Matvejev S.D. - The Serbian Academy of Sciences and Arts, 1976. Monographs 491. Beograd.
Matvejev S.D., Vasič V.F. Catalogus faunae Jugoslaviae, Aves IV/3. Academia Scientiarum et Artium Slovenica. Ljubljana, 1973.
Mayr E.    Princiées of Systematic Zoology. New York, 1969.
Patev P. — Zool. Institut i Muzey BAN. Sofia, 1950.
Stepanian L.S. - Zool. Žurn., 1972, 51, N 9.

FOLK AND ONOMATOPOEIC NAMES OF BIRDS

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The round table discussion "Folk and onomatopoeic names of birds"
( held on August 17 ) was actually dedicated to the trends of biolinguistics.
connected with the human imitation of birds voices and the origin
onomatopoeic names of birds. Ornithologists, specialists in bio-
acoustics and linguists of the USSR, Great Britain, GDR, FRG and other count-
ries took part in the discussion.

Studies on onomatopoeic names by the method of biolinguistic parallelisms
involve comparative investigations in various languages and linguistic groups,
and this is impossible without close cooperation of scientists of various
countries.

The convener of the discussion O.L.Silajewa in her opening address marked
the importance of studying and bringing out folk and particularly onomato-
poeic names of birds, being a treasurehouse of every modern language, spoke
about the method of interlingual parallelisms (first developed by G.Demsntiev
and V.Ilyichev in 1963), outlined the prospects of further studies on biol-
ingustic parallelisms in their association with attractive and repellent
means of controlling the behaviour of birds. The work by V.Ilyichev and
O.Silajewa extended the investigations in this direction. However, the prob-
lem of onomatopoeic names, its relation to the imitation of human voice by
birds and the formation of contacts between man and birds on this basis is
so complex and many-sided that it requires efforts of many researchers of
various specialities. This problem is in the scope of a new scientific
fisld - biolinguistics, which was officially recognized at the International
Symposium on Biolinguistics in GDR in 1976. Specifically, biolinguistics which
appeared at the junction of biology, linguistics and mathematics, deals with
the solution of practically important problems of controlling the behaviour
of animals, input of speach information into a computer, pediatric pathology
and clinical cases. Ornithological bioacoustics and biolinguistics are of
great interest for general biolinguistics since these trends are associated
with acoustic communication between man and birds, with the control of
birds' behavior and to a certain extent with that influence which the envir-
onment, birds' voices in particular, exerted on the formation of acoustic
behaviour of man (languages, folk music).

W.Zimdahl, being a linguist and editor of the journal "Der Falke"(GDR)
made a report on the distribution of dialectal variants of some birds' folk
names in different regions of GDR and on the coincidence of the area where
the species is distributed with the area where the corresponding dialectal
name is used. Using the comparative historical method in linguistics it is
possible by investigation of dialectal and archaic names to establish the
fact and approximate boundaries of the distribution of a species which no
longer occurs in this region.

English bioacoustic J.Boswell in his report considered various methods
and objectives of imitating birds' voice by man and the relation of this
imitation to onomatopoeic names. He demonstrated the effect of some decoy

devices. The participants of the meeting listened with great interest to recordings of folk and classical music which included birds' songs.

Ornithologist and bioacoustic H.H.Bergmann (FRG) in his brief communication expounded some of the results of his joint investigations with H.W.Helb (FRG) in the field of recording, sonographic analysis, and cataloging of the voices of European species of birds, as well as comparative analysis of their calls with interjectory-lexical imitations and morpheme imitations of birds' acoustic calls by man. Special emphasis in the investigations of these scientists is placed on the formation of folk names of birds based on the voice of a corresponding species.

Many scientists participated in the discussion of the reports, including B.Veprintsev, G.Grempe, M.Lebedeva, I.Nikolsky, A.Tikhonov. The participants outlined the prospects of contacts between ornithologists, specialists in bioacoustics and linguists of various countries, pointed out the necessity of consolidating the efforts of these specialities for the solution of theoretical and practical problems of ornithological biolinguistics. They outlined the following problems of applied ornithological biolinguistics: unification of folk and scientific names of birds, study, development and improvement of acoustic contacts "man - bird" in order to control the behaviour of birds.

Discussion O.L.Silajewa:

The basis of onomatopoeic names is occasionaly the onomatopoeic interjections of "co-co", "croak-croak", "chirp-chirp" type. Only later they got the form of onomatopoeic nouns (the birds' names) and verbs, which expressed the birds' voice activity. These words got the onomatopoeic elements for expression of grammer categories(especially in inflected languages). Namely these later layerings differentiate the onomatopoeic names in different languages. It may be so that the "cockoo" was marked by the interjection "co-co" and the "crow" by "cro-cro" in the ancient language. In the early stage of the development and because of the proximity to the nature the man had more opportunities for imitation of nature sounds, and in particular birds' voices; his vocal organs were better adopted for this activity. On the other hand the nature sounds stimulated much the formation of man's acoustic behaviour, as the nature and its sounds played a great role in the life of an ancient man. The man enriched his poor vocabulary by hearing the rustle of the leaves, the babble and twitter of birds, the murmur of a brook and the growl of a dog. The sound form of these words had a direct connection with the meaning, marked by this combination of phonemes. The onomatopoeic phonemes are scattered in the lexicon:"ss" - the hiss of a snake; "zz" - the buzz of a bee or a beetle; "wh" - the whistle of the wind (in my native language it would be easiar for me to give such examples).

The onomatopoeic names were not only of the nominative function, but they were also used by the ancient man as sound decoyes. In such a way it was made a beginning for the control of birds' behaviou·.

The convener of the discussion is thankful to all its participants, and besides to I.D.Nikolsky, for assistance in preparing and operating sound reproducing equipment.

WORKING GROUP ON CRANES OF THE USSR
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In spite of general sympathy with cranes it is only sporadically that they have become the subject of special studies. The increasing rarity of these birds has been accepted as something regular and inevitable. The turning point came in the 1970s and coincided with the period of search for active forms of protecting rare species. The rescue of the whooping crane from what seemed to be the inevitable extinction jolted ornithologists out of a state of reflection. The experience gained was widely employed for the elaboration of the "Sterkh" (Asiatic white crane) program. This program had no analogs in the scope of tasks and methods of their solution. Information on the wintering of a very small isolated group of Asiatic white cranes which presumably nested in the lower course of the Ob river gave a direct impact to its elaboration. The program was not confined to the protection of the local population alone, but rather was aimed at radical improvement of living conditions in the nesting part of the area, in wintering places and along migratory routes, as well as at increasing their numbers and distribution range.

Coordinated efforts of specialists from the USSR, USA, India, Iran and JCF have made it possible to clarify the previously unknown biological aspects, to find new regions of nesting and wintering of Asiatic white cranes, to grow successfully birds from eggs brought to JCF nurseries and Ob reserve from the Yakutsk ASSR, and obtain their progeny. This program alone required considerable efforts and expenses, and the realization of the first (return of the progeny from the birds grown from eggs to nature) required 10 years.

Simultaneous elaboration of similar programs for other species presented extreme difficulties. At the same time a delay led to the death of habitats of some populations. The situation with Japanese cranes was particularly grave. Uncoordinated attempts of some enthusiasts failed to stop a catastrophic drop of their numbers. The situation with other, even relatively numerous species was not much better. Uncertainty of the situation, lack of data on the condition of some species, on the direction, rate and causes of changes in their populations gave rise to particular concern. Extremely contradictory information was published with much delay and could not be used for prompt solution of urgent problems.

All this was the main reason for holding a meeting of specialists and public representatives concerned with the fate of Japanese cranes at the Biological Department of the Moscow State University in spring of 1980. The participants were able not only to elucidate a number of problems vital for this species, but also to arrange for cooperation in their solution. Thanks to this, it was possible in a short time to define the area and the numbers of the species, to arrange a regular examination of some habitats, to find out specific nature of limiting factors, to begin a systematic study on their biology. In a number of regions it was possible to drastically low the influence of fires and other forms of human interference on nesting areas. As a result, the number of nesting

birds in the Arkharinskaya lowland alone rose from 3 in 1979 to 26 pairs in 1984, while the total number of Japanese cranes here reached 126.

However the significance of this meeting went far outside the scope of one species. Having marked the scarcity of knowledge about cranes and the inefficiency of the current protecting measures, the participants adopted a decision to organize a Working group on cranes (WGC). This marked a qualitatively new stage in the study and protection of birds in the USSR. WGC set the objective to cooperate with all the organizations and people concerned with protecting all the species of cranes of the fauna of the USSR. To achieve this aim WGC renders a comprehensive assistance in organizing regional divisions, in collecting and transferring information on the locality, number and biology of cranes, in organizing and conducting investigations to study certain species and their habitats, in developing and providing the most efficient measures to protect cranes and their habitats, in conducting educational work and popularization in the field of protecting cranes through radio, television and press, in publishing science popular literature dealing with biology and methods for protecting cranes.

Any citizen of the USSR concerned with protection of cranes and ready to take part in their studies can enter the membership of WGC. Among 100 members of WGC, apart from ornithologists and specialists in the field of environmental protection there are people of various professions, students and school children. The Bureau and Curators are the authorities of WGC. The Bureau of WGC is in charge of general direction and current organizing activity, renders assistance in organizing the protection of territories, meetings, published materials of WGC and supervises the fulfilment of decisions.

The Curators responsible for various problems, species and regions play an increasingly important role.They actively participate in the elaborations and coordination of long-term research programs and concrete measures for protecting cranes, promote their realization, render necessary assistance for WGC members, advocate popularization and arrange educational work.

The plans for various measures and the composition of the governing bodies are approved at WGC meetings. The subjects of their discussion clearly reflect the main stages in the development of WGC. While the first meeting of WGC delt only with the condition of Japanese cranes, the second one, held a year later at the Zoological Institute of the USSR Academy of Sciences (Leningrad), considered practically all the available information about the numbers and distribution of all species of cranes in the USSR and their protection in certain regions of the country. This made it possible to evaluate the condition of cranes in the USSR and elaborate the Program of their investigations. Information on all the changes in the condition of certain species became the indispensible subject at all subsequent meetings.

The third meeting held in 1982 in Oka reserve was mainly devoted to the universal methods of investigation and particularly those taking stock of birds' numbers. This was associated with the lack of specialists having experience in practical work with cranes and in regional specific of carrying out investigations. At this meeting the members of WGC not only heard and discussed the reports but also obtained consultations on the practice of keeping cranes in the Nursery and on breeding them in the Oka reserve.

Practical knowledge was further enriched during IV meeting in the Matsalu reserve (Estonian SSR). It was dedicated to studies on migrations and mass accumulations of common cranes. The participants jointly took stock of cranes of the largest (12 thousand individuals) autumn aggregation in Europe, familiarized themselves with the station of radio detection and location of migrating cranes and computerized treatment of phenologic data. The places for holding meetings are chosen so as to enable the participants to get acquainted with the most important regions of cranes' habitats, the regional specific of their studies and protection, the most interesting trends of investigations. At the same time this facilitates the solution of practical problems, contributes to the popularization of WGC activity and to the involvement of new members into WGC.

All the scientific information is published in collected works of WGC which are subject-oriented. The first two issues "The Cranes of East Asia" and "The Cranes of the USSR" - contained data on the distribution and numbers of cranes in the USSR. Of special value are the data on wintering places of cranes in the USSR, obtained due to cooperation with JCF. Three more issues dealing with methods of studying cranes in nature and their breeding in confinement, with problems of the biology and morphology of cranes, with common cranes have been prepared for publication. They also contain data on the condition of cranes.

Apart from this the activity of WGC is described in the regular Bulletins of WGC, in "Zoological Journal" and in the journal of "Hunting and Game Management". This provides the members of WGC and wide sections of the populations with timely information about various events and measures of WGC.

The coordinating activity of WGC, selection of the most important subjects of studies with due regard for the interests and professional level of executors made it possible to obtain in a short time information on the conditions and biology of cranes, greatly surpassing all that had been previously known. Cranes have become a model group in the solution of many general problems. A number of sanctuaries have been created for the protection of cranes in the Far East Maritime and Khabarovsk territories, in the Moscow, Amur and Chita regions, in the Yakut ASSR, in the lower course of the Ob river in the Baltic Sea region.

International cooperation is steadily progressing. Specialists from the USSR, Japan, China participate in the joint program of coloured banding of Japanese and white-naped cranes, and in 1984 Japanese cranes were taken stock of for the first time in all the sections of the nesting area. In the Oka reserve common cranes are colour banded. In 1985 two eggs of Asiatic white crane obtained from JCF were placed in the nests of common cranes.The nursery for crane breeding and the Moscow Zoo exchange cranes with JCF, thereby making it possible to diversify the genofond of cranes kept in confinement. The protection of cranes is widely popularized. Six documentaries with participation of WGC, the members of WGC regularly broadcast lectures by television and radio. The membership of WGC is constantly growing, being filled up mostly with young people. The scope of interests and problems tackled by WGC is continuously expanding. The main point of this resides in the fact that the activity of WGC promotes the formation of qualitatively new relations between people and cranes.

MORPHOFUNCTIONAL ORGANISATION OF THE VISUAL
SYSTEM IN BIRDS
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Several (up to seven) structurally and functionally distinguished channels of transmission and processing of the optical information have been differentiated in the pigeons, fowls, crows, some small passerine and predatory birds using the complex of the behavioral and conditioned reflexes methods in combination with morphological and electrophysiological investigations. Relative development of these channels varies in different species.

Geterochronous maturation of the neurons and synaptic connections belonging to the separate pathways and levels of visual analysatory system was revealed in the course of the brain ontogenesis. Tectal and accessory optic connections are formed in birds at the time of hatching. They become involved in the conduction of the signals necessary for fast eyes and head turning towards attractive cues, for moving stimuli tracking and related nystagmus. The development of regular visual projection to the telencephalic hyperstriatal region terminates later. This projection is related to the neurophysiological mechanisms of the memoryzation or imprinting of biologically significant cues on the basis of differentiation of the shape, size, orientation and some other features of stimuli. The involvement of the area Wulst in the neural organization of the avoiding and attacking (pecking) reaction as well as gaze fixation on the certain details of the visual surrounding have been shown. Hyperstriatal efferents influence the activity of the neurons in the tecto-ectostriatal system, which is presumably involved in the regulation processes of detection and localization of the objects in the visual field and thus provide suitable orientation of the bird in space.

Recordings of locomotory activity of the chaffinches, robins, some other migrants and pigeons exposed under natural sky and in planetarium have shown that choosing and maintenance are seasonally constant and homing direction of the movement is performed by using the system of time counting, which includes pineal body and suprachiasmatic nucleus of the hypothalamus. Integration of the descending influences from this system with signals from visual centres at the level of the segmental and motor brain stem nuclei is necessary for the compensation of the right-sided displacement of the most bright sector above the horizon with a velocity near 15 deg. an hour. The community of mechanisms of day and night astroorientation in this aspect has been suggested.

# INTERRELATIONS BETWEEN THE COMMON CUCKOO AND ITS HOSTS IN THE TERRITORY OF THE USSR

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The attachment of cuckoos to a certain host is maintained from generation to generation by the contact ways due to which arise the intraspecific biological groups (populations) of cuckoos each with its particular hosts. Stability rate of these connections with the different foster parents is unequal and can serve as a remoteness rate index of these new relations. The spatial distribution of Cuckoo biological groups is far from being clear particulary for easten parts of the range.

The authors collected, in all, 1826 records of the cuckoo's eggs and young in the nests of 104 species of small passerines adding to literature their own observations and the information from a number of ornithologists. Motacilla alba, Phoenicurus phoenicurus, Erithacus rubecula, Acrocephalus arundinaceus are the species most frequently parasitized (most frequently rearing the common cuckoo's young) in the USSR (more than 50 per cent of all findings). With 18 species the contacts are occurring more locally. The rest 82 species are occasionally cuckoo's hosts.

The common cuckoos laying clear light-blue eggs parasitizing Phoenicurus phoenicurus inhabiting pine forests form the most distinct race Saxicola rubetra, S.torquata must be evidently its secondary hosts.

The coloration of the eggshell cannot permanently serve as a race character. Even in the nests of primary hosts occur the cuckoo's eggs of various types.

In the regions with great concentration of initial hosts the percentage of "cuckolded" nests varies between 40 (Phoenicurus phoenicurus) and 90 (Motacilla alba) per cent. The change of the host concentration places brings the cuckoo spatial moving. This fact shows the brood parasite populational structure range mobility.

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## CONTENTS